

# THE STRUCTURE AND ECOLOGY OF LOW ISLES AND OTHER REEFS

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WITH FIFTEEN TEXT-FIGURES AND TWENTY-SEVEN PLATES.

## CONTENTS

	PAGE
PREFACE . . . . .	17
PRELIMINARY DESCRIPTION OF THE REEFS . . . . .	22
THE ECOLOGY OF LOW ISLES . . . . .	35
REVIEW OF THE LOW ISLES FAUNA AND FLORA . . . . .	69
COMPARISON OF THE ECOLOGY OF OTHER REEFS WITH THAT OF LOW ISLES . . . . .	80
SUMMARY AND CONCLUSIONS . . . . .	93
A COMMENT ON THE INSTRUMENTAL SURVEY . . . . .	99
APPENDIX . . . . .	101
REFERENCES . . . . .	102
INDEX TO PLANTS AND ANIMALS . . . . .	106

## PREFACE.

(By T. A. STEPHENSON.)

THE ecological field-work upon which this paper is based was carried out under my direction by several members of the Expedition. The instrumental surveys of Low Isles and Three Isles to which we owe our knowledge of the physical features of these reefs were executed by M. A. Spender working for the Royal Geographical Society; he was assisted by Anne Stephenson and their results are embodied in Plates I and II.\*

\* For the presentation of data in the text-figures, however, and in those of the uncoloured plates, which are reproduced from drawings and not from photographs, I am responsible.



TEXT-FIG. 1 (for description, see p. 19).

The ecological work was carried out by the authors with the assistance of F. W. Moorhouse in the earlier stages and of E. A. Fraser, S. M. Manton and J. S. Colman later on. We are very much indebted to all these workers for their co-operation. We are also under a debt of gratitude to Mr. George Butler, of Townsville, owner of the motor-launch "Tivoli," to whose skill in navigation and other matters we owe the success of our visit to Lizard Island and the Outer Barrier; and to Mr. Wishart, of the yacht "Luana," who took us to Three Isles. Mr. T. C. Roughley has kindly allowed us to reproduce some of his photographs in our plates. Our work has also been greatly assisted by the very fine series of aerial photographs of Low Isles taken for us by the R.A.A.F. A mosaic from some of these is reproduced in Plate XXVII. To the Royal Geographical Society we are indebted for permission to reproduce Plates I and II, and Text-fig. 7, which (with the exception of the central section in Text-fig. 7) have appeared before in the Geographical Journal.

A short account of early references to Low Isles in the literature is given by Spender (1930, p. 212) elsewhere, and we need mention here only the facts that this island-reef was first mentioned by Cook in the journal of his historic voyage of 1770, and that the first investigators to visit it were J. Macgillivray and Thomas Henry Huxley, aboard H.M.S. "Rattlesnake" under Captain Owen Stanley, in 1848.

Since the whole work of the expedition was directed towards the elucidation of problems which have a direct bearing on ecology (*i. e.* towards a study of conditions and food-supply in the sea, of the feeding and metabolism of corals, of the growth and breeding of marine organisms, and so forth), it was clearly essential that the populations of the reefs themselves should be studied in such a way that, before correlating and applying the results of all the special lines of work, we should acquire a knowledge of what organisms form the bulk of these populations, and in what manner they arrange themselves with respect to one another and to their environment.

The descriptions of the distribution of organisms on the reefs are not the expression of individual opinions as to the nature of the populations, but are based upon a systematic survey carried out by several workers who wrote an agreed statement of their results at the end of each field excursion. Our examination of Low Isles was much more detailed than that of the other reefs; here the reef was divided up into small areas, and each of these was studied in turn by at least two workers, who made a description of each patch, and also lists and collections of the organisms found in it. The survey was therefore to some extent quantitative, and the personal element was eliminated as far as possible. The aims in collecting were (1) to secure a series of specimens of any common organism, the name of which was not certainly known, so that it might be identified later; (2) to obtain a representative collection of the common organisms, each labelled with some symbol indicating the exact area and habitat from which it came; this collection to be deposited in the British Museum for future reference, so that any statement of the

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TEXT-FIG. 1.—Diagram of the Great Barrier Reef from Cook's Passage to Trinity Opening, showing the positions of the reefs described in this report, and suggesting the differentiation of the reefs into three series (Outer Barrier, Inner Reefs and Island Reefs), which is recognizable north of Trinity Opening (see p. 90). The High Islands are distinct from any of these series, being isolated mountains. Note the position of the 100-fathom line, which begins to diverge from the reefs just north of Trinity Opening. Modified from Admiralty Charts nos. 2923 and 2924.

occurrence of a given species on the reef should not depend on our word alone, but should be verifiable.

This method was designed for a general study of a wide area, and not for the precise estimation of the population of a small one. I therefore planned from the beginning to illustrate it by a series of accurate quantitative studies in chosen strips or patches of the main area. The result of such of these studies as we were able to make is recorded in a separate paper in this volume.

The general survey is subject to certain qualifications. The method outlined above could not be carried out as completely as we wished, because of the pressure of other work; but we believe it to have been sufficiently thorough to justify the account here given. Certain fields were perforce omitted from our scope. We could not give much attention to the concealed and commensal life of the interstices of coral platforms and of living corals; nor to the boring organisms; nor to the fishes; because any one of these would have occupied all the time at our disposal. But our omissions in these directions have been supplied to a considerable extent by G. W. Otter and G. P. Whitley. Some allowance must be made for the fact that the survey necessarily covered several months, and there would therefore be seasonal variations during its period. This is, however, probably of little importance from the point of view of this report, and mainly affects the size and number of some of the algae. Lastly, the omission of any extensive discussion of physical and chemical factors in the environment is intentional, since these will be treated fully in later papers dealing with the life and growth of corals.

There has been a tendency in recent years to regard the coral reef problem as one which is primarily of a geographical nature. The work of the Barrier Reef Expedition swings the centre of interest back towards the biological side, and our ecological study of Low Isles is a development of the methods by which the classical studies of coral reefs, such as those of Funafuti and the Maldives and Laccadives, were made; it is also in line with recent American work, and with that of Umbgrove and others. It is a method involving close collaboration between the surveyor of the physical features and the worker who is examining the plant and animal communities; and we feel that before it will be possible to review coral reefs in general with precision and security, this twofold point of view will need to be applied more widely.

There are several advantages to be derived from a careful study such as the one made at Low Isles. In the first place, only a detailed instrumental survey involving accurate measurements and determinations of levels can make it possible to form, after one's return from the field, a true conception of the inter-relation of the parts of a reef, both in the horizontal and vertical senses; and to describe accurately the distribution of organisms on it, especially as regards their zonation according to level and their relation to states of the tide. Secondly, such a study provides a real basis for the comparison of the reef with others; without exact data of distances, heights and populations, as well as details of the substratum, comparison must be a matter of uncertainty. Lastly, there is the advantage that anyone who has undergone the discipline of a detailed study of one reef, is thereby enabled to visit profitably other reefs which he cannot examine for more than a short time. His training has enabled him to appreciate rapidly the essential points involved, and to assess the relative importance of the surface-features accurately; whereas anyone without such experience is liable to be bewildered on a short visit to a reef, and to carry away no true impression of its formation. The incidence of the biological side of

the training lies in the fact that the differentiation of the zones and regions of a reef is often very subtle, and some pre-existing knowledge of the characteristic distribution and relations of common organisms may give a geologist or a geographer the key to some variation in the surface morphology of a reef which, though not easily appreciated at first sight, may be fundamental.

The lists of plants and animals presented in this paper, in connection with some of the regions described, make no pretence to be complete lists of the organisms found in the localities in question, nor even of the common ones. We could add to them extensively from our notes and collections; but have intentionally curtailed them because their object is purely illustrative. They are designed to convey in a summary form an idea of the series of organisms which characterize the various zones or areas, and this they effect as accurately in their present form as if they were extended.

Further information regarding the field-work upon which this paper is based may be obtained as follows by anyone desiring it: The data obtained by Spender during the instrumental surveys are deposited with the Royal Geographical Society, and include information not published either here or in the *Geographical Journal*. A set of prints of the aerial photographs of Low Isles is in the British Museum (Natural History), as also are the ecological collections. For further data referring to plants application should be made to G. Tandy, British Museum; for information referring to animals, to T. A. Stephenson, Zoology Department, The University, Cape Town.

For the identifications of the organisms mentioned in the report we are indebted to the specialists who have determined the collections for us, and who have been of great assistance to us in a variety of ways. The several groups have been determined by the following workers. I have worked carefully through all the collections of animals myself, after the identification of the species, in order to check and correlate the observations made in the field.

#### PLANTS.

FLOWERING PLANTS.—A. W. Exell, E. G. Baker, G. Taylor, J. E. Dandy and G. Tandy, British Museum.

ALGAE.—G. Tandy, British Museum.

#### ANIMALS.

PROTOZOA.—(Foraminifera). E. Heron-Allen, British Museum.

PORIFERA.—M. Burton, British Museum.

HYDROIDA.—E. A. Briggs, University of Sydney; and A. K. Totton, British Museum.

SCYPHOZOA AND ANTIPATHARIA.—A. K. Totton, British Museum.

ALCYONARIA.—S. J. Hickson, University of Cambridge.

ACTINIARIA and allied forms.—Oskar Carlgren, The University, Lund; and T. A. Stephenson, The University, Cape Town.

MADREPORARIA (and *Millepora*).—G. Matthai, Government College, Lahore; and T. A. Stephenson, The University, Cape Town.

NEMERTINEA.—H. A. Baylis, British Museum.

POLYCHAETA AND GEPHYREA.—C. C. A. Monro, British Museum.

OLIGOCHAETA.—J. Stephenson, British Museum.

ASTEROIDEA.—A. Livingstone, Australian Museum.

ECHINOIDEA, OPHIUROIDEA, HOLOTHUROIDEA AND CRINOIDEA.—H. Lyman Clark, Museum of Comparative Zoology, Harvard.

CIRRIPIEDIA.—R. Bassindale, The University, Sheffield.

ISOPODA.—M. H. Hale, The Museum, Adelaide, S. Australia.

AMPHIPODA.—K. H. Barnard, S. African Museum, Cape Town.

CRUSTACEA DECAPODA.—F. A. McNeill, Australian Museum; and Isabella Gordon, British Museum.

HYMENOPTERA.—H. Donisthorpe, British Museum.

LEPIDOPTERA.—N. D. Riley, British Museum.

DIPTERA.—Daphne Aubertin, British Museum.

ARACHNIDA.—Susan Finnegan, British Museum.

GASTROPODA AND LAMELLIBRANCHIA.—T. Iredale, Australian Museum; and J. R. le B. Tomlin, British Museum.

ASCIDIACEA.—Anna B. Hastings, British Museum.

POLYZOA.—Anna B. Hastings, British Museum; and A. Livingstone, Australian Museum.

ENTEROPNEUSTA.—Ethelwynn Trewavas, British Museum.

PISCES.—G. P. Whitley, Australian Museum; and J. R. Norman, British Museum.

AVES.—N. B. Kinnear, British Museum.

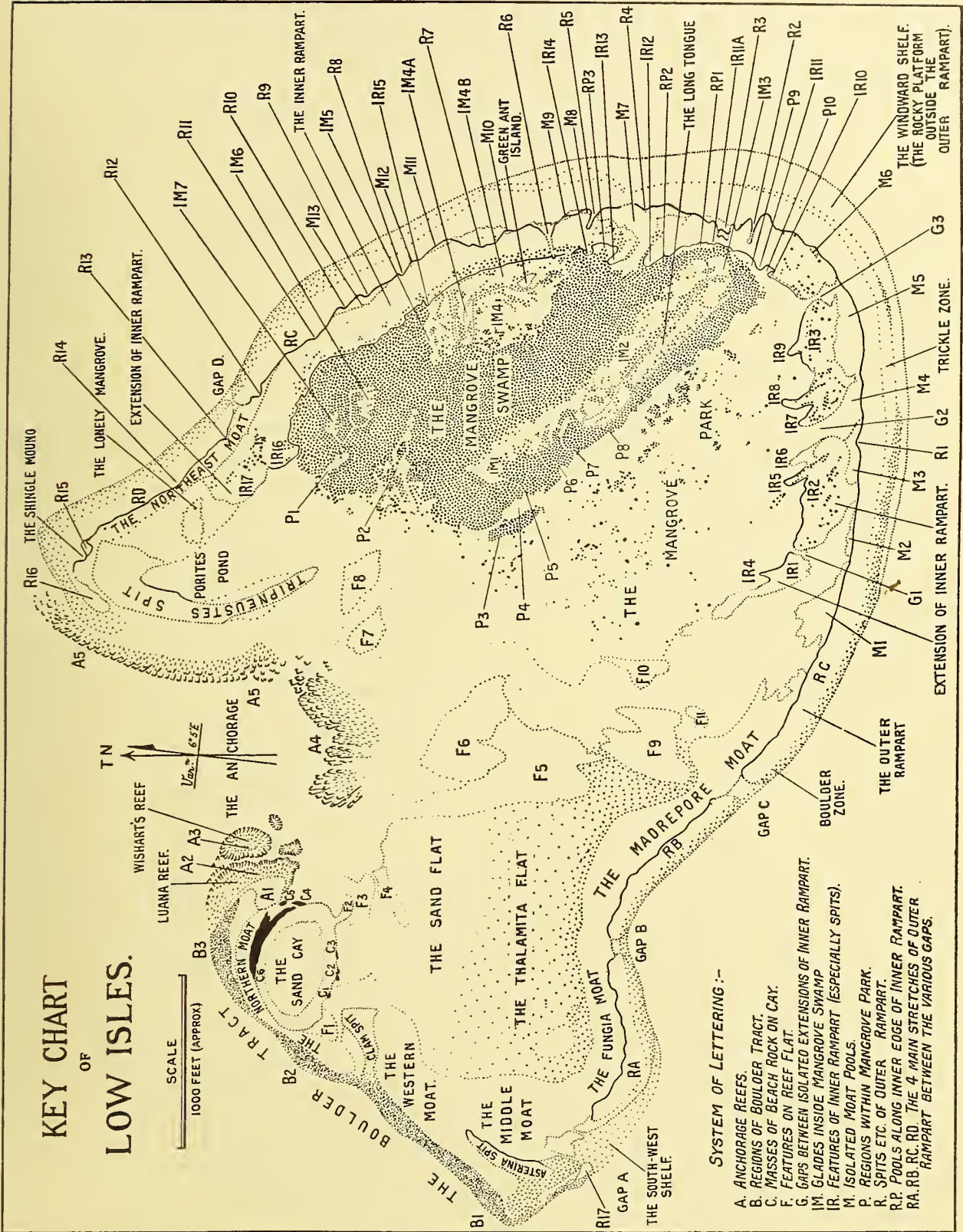
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## PRELIMINARY DESCRIPTION OF THE REEFS.

(By T. A. STEPHENSON, G. TANDY, and M. A. SPENDER.)

In order that the following description may be the better appreciated, two general influences should be kept in mind from the outset. The first is that of the tides. The tidal ranges may be accepted as the same for all the reefs to be considered. It is necessary when recording tidal variations to refer the level of the sea to the level of some fixed point. The fixed point (datum) which was used at Low Isles was that established during the survey by H.M. Surveying Ship "Penguin" in 1905. This was the level of the lowest available tide, and was measured as 17 ft. 2 in. below the level of the top of the step at the entrance to the Low Isles lighthouse. To this level all soundings and measurements of height recorded in this paper are referred. The highest tide measured on the continuously recording gauge employed by the expedition was 10 ft. above datum, and the lowest 0.4 ft. below it. The term "spring tide" will here be used to denote a tide which approaches the extreme range of 10 ft., and "neap tide" for one with a range of 2 ft. or less.

A second influence of prime importance is that of the prevailing wind (Text-fig. 3). For the period of twelve months during which our observations were made, the integrated mileage of wind recorded in the south-east quadrant is 85% of the total (a wind-rose is included on Plate I). During the summer months the south-east wind does not blow with any regularity, but there is no true reversal to a north-west monsoon. This is sufficient, for our purposes, to justify the use of the term "south-east trade wind."



The situations of the reefs to be described are indicated in Text-fig. 1. These were chosen for description because they illustrate the principal types of reef found within the area studied by the Expedition, and because, as will appear later, they seem to form an ecological series.

A. LOW ISLES. Lat. 16° 23' S. (Text-fig. 2 ; Plates I and III, etc.)

The name "Low Isles," in origin descriptive, was given to a small vegetated island together with a neighbouring mangrove-swamp, which are situated some seven miles from the mainland, and about 35 miles\* north of Cape Grafton. The swamp and the island lie upon a single reef, and the name "Low Isles" will be used in this paper as referring to the whole system, including the reef itself and the structures upon its surface. The nearest of the large reefs of the Barrier series lies some seven miles to the eastward. Low Isles, therefore, is an isolated reef, situated in a shallow sea, and is not exposed to the surf of the Pacific. The sea in its immediate vicinity is from 8-14 fathoms in depth.

The reef has a major axis of about one mile, and the greater part of it is submerged at high water. It possesses a number of well-defined surface features, and these, both in form and orientation, express the dominating influence of the south-east trade wind. These regions, which are indicated in Text-fig. 2, will now be described.

1. THE SAND CAY.† (Plate IV, fig. 1.)

The islet on which the lighthouse stands. It lies at the leeward or north-western extremity of the reef, and is a flat-topped mound of sand, some 3½ acres in extent, supporting a dry-land flora and fauna. Its greatest height is 16 ft. above datum.

2. THE MANGROVE SWAMP. (Plate V, fig. 1 ; Plate VI, figs. 1 and 2 ; Plate VII, figs. 3 and 4.)

An area covering about 50 acres, the greater part of which is thickly wooded with mangroves, of which *Rhizophora mucronata* is the dominant species. The woodland includes a number of glades or open spaces in which different conditions prevail.

3. THE SHINGLE RAMPARTS. (Text-fig. 7.)

A. *The Outer Rampart* (Plate XI ; Plate XII, figs. 1 and 2 ; Plate XIII, fig. 1).—A ridge of shingle consisting of dead coral fragments. This material is heaped up about the rim of the reef to form a band, shaped like a horse-shoe, with its convexity towards the south-east. The limbs sweep round to leeward, embracing the general reef flat upon which are situated the mangrove-swamp and sand cay. The inner edge of the rampart is sharply defined, forming a steep escarpment varying in height from about 2-4 ft. ; but towards the sea it slopes gradually downwards and merges into the seaward slope of the reef. It extends from the gap A of the key chart to the Shingle Mound, and in its south-eastern part it attains a height of 7½ ft. above datum. Along the south-western margin of the reef it is lower, and is covered by tides rising 5 ft. above datum.

B. *The Inner Rampart* (Plate XII, figs. 1, 3, 4 ; Plate XIII, figs. 1-3).—In the space between the outer rampart and the mangrove swamp lies a second band of coral shingle

\* Distances are given in sea miles.

† The word "cay" is derived from the Spanish "cajo," a shoal; in the West Indies the derivative used is "key."



about 200 ft. wide, in form similar to that already described. It follows the trend of the outer rampart fairly closely, and is continued beyond the mangroves in either direction as patches or islands of shingle. It differs from the outer rampart in that the shingle is everywhere more or less compacted together by means of mud and silt which occupy its interstices. In the extreme case the shingle and mud is concreted to form a hard rock, which will be termed in this paper *shingle conglomerate*.

#### 4. THE BOULDER TRACT. (Plate V, figs. 3 and 4.)

A band of boulders and large fragments of coral rock\* extending from the western corner of the reef (B1 on the key chart) to the anchorage. It stands in the same relation to the reef-flat as does the rampart elsewhere. The boulders are frequently 3 or 4 ft. high.

#### 5. THE REEF FLAT.

The whole area included by the outer rampart and the boulder tract. It is by no means uniform in structure and appearance. At the lowest ebb of a spring tide, the level of the flat is well above that of the sea outside the rampart; much of the eastern part is then 4 ft. above datum, or but little less (Text-fig. 7). Such parts of the flat as are not exposed at the ebb as wide sandy, rocky, or boulder-strewn expanses are covered by shallow water, which in places is as much as 2 ft. deep, but commonly much less. There are, therefore, discontinuous pools on the surface of the flat, but nothing exists which can be properly described as a lagoon. For convenience of reference, the flat may be subdivided as follows:

(a) *The Sand Flat* (Plate VIII, fig. 1).—An area of sand with shallow pools, continuous with the sand cay.

(b) *The Thalamita Flat*.—An area to the south of and not sharply delimited from the sand flat. Its characteristic feature is the presence of numerous slabs and boulders of coral rock with sand and small pools between them.

(c) *The Mangrove Park* (Plate XIII, fig. 4).—A large area to westward of the mangrove swamp, in which shallow pools predominate, and over which a considerable number of isolated trees of *Rhizophora mucronata* are distributed. Many of these are young, and there are also clumps of fairly large trees; but they nowhere attain the dense formation characteristic of the mangrove-swamp proper. The ground is partly sandy, partly overlaid by flattened and much honeycombed coral rock; and is for the most part more or less thickly colonized by a flowering plant with grass-like leaves (*Thalassia Hemprichii*), with which other plants mingle to form a turf.

(d) *The Moats* (Plate VIII, fig. 3).—A linear series of pools lying immediately within the outer rampart or the boulder tract. They are nowhere more than about 18 in. deep at low water. Inside the boulder tract and the western part of the outer rampart, these pools form a single continuous moat or band of water; but from the southern extremity of this band onwards (following round the rampart in an anti-clockwise direction) the moat becomes much interrupted, and is represented only by a chain of discontinuous pools until it re-emerges, near the northern extremity of the mangrove swamp, as a second band-like sheet of water (the north-west moat). The several regions of the western and principal stretch of the moat have been given individual names (Northern Moat, Western Moat, Middle Moat, etc.) for convenience of reference.

\* A list of the types of rock mentioned in this report will be found in the appendix, p. 101.

## 6. THE ANCHORAGE (Plate XIV, fig. 1).

A bay or indentation in the northern side of the reef. It has depths of 10 to 20 ft. below datum, a sandy bottom, and is fringed by reefs supporting a rich growth of living coral.



TEXT-FIG. 3.—A diagrammatic representation of the effect produced by the Low Isles Reef upon the waves driven against its windward arc by the south-east trade wind. This figure throws light upon (a) the general shape of the reef, and (b) the formation of the cay, which appear to be due to the united effects of the system of waves here shown, and of the eddy set up in the lee of the reef by the general drift of water before the south-east trade, especially on the flood tide. The data are obtained from a series of aerial photographs taken by flight 101 of the R.A.A.F. in September, 1928.

It will be appreciated that at high water of springs the entire reef flat is covered by about 6 ft. of water. Only the upper part of the sand cay and the main foliage of the

mangroves then appear above the sea, the two being separated by a broad sheet of water. The general aspect of the system at low water of springs is very different; the sand cay is then a hummock from which one can descend on to the reef flat and walk across to the mangroves, or to the south-eastern corner of the reef. The rampart has emerged from the sea and can be seen encircling the reef as a low wall, rising to 10 ft. above datum at its north-eastern extremity in the Shingle Mound (Plate XII, fig. 2).

All tides do not ebb to the same level, and this fact conditions the amount of the anchorage and seaward slope accessible at low water. The zones of rich coral growth are exposed at extreme low tides only. During the winter months (May to October) the lowest tides occur during the daytime, for several days in each month, towards the time of new moon. In the summer the opposite is the case, the lowest tides occurring at the time of full moon, and at night. Extreme exposure, therefore, never occurs in daylight during the hottest weather.

### B. THREE ISLES. Lat. $15^{\circ} 07'$ S. (Plate II.)

Three Isles is a group of three low islets lying some 8 miles NE. by N. of Cape Bedford. These islets are part of a single reef-system directly comparable with that of Low Isles. The system lies about 80 miles north of Low Isles, and is similarly situated with respect to the mainland and to the Barrier Reefs, the mainland lying about 10 miles to the westward and the inner reefs of the barrier some 4-6 miles to eastward. The protected sea surrounding the reef is of the same depth as at Low Isles, the tidal range and establishment are similar, and the south-east trade wind is equally dominant, though fresher and more persistent.

In essential form Three Isles and Low Isles are so much alike that the resemblance can be traced in some detail. The plan of Three Isles is ovate, the broad end to windward. In this it is probably a more usual and regular example of the class of reef to which it belongs than Low Isles, which possesses, in its western salient, a feature peculiar to itself. The apparent difference between individual features on Three Isles and Low Isles is in some cases considerable, but a close analysis reveals their essential similarity; the regions will be considered under the same headings as for Low Isles.

#### 1. THE SAND CAY.

The sand cay is about 36 acres in extent and about 3 or 4 ft. higher than that of Low Isles.

#### 2. THE MANGROVE SWAMP.

At its northern end this lies close to the sand cay. It covers some 41 acres, and its limits are very clearly defined. The whole inner structure of the area is not known, but it contains glades similar to those at Low Isles. As will be obvious from the figures given, the mangrove swamp is smaller than that of Low Isles, whilst the cay is considerably larger.

#### 3. THE RAMPART.

This is less well developed than that of Low Isles; it is nowhere very high—probably rarely more than 5 ft. above datum. It is somewhat broken in the south-eastern part of its circuit, where the counterpart on Low Isles is particularly free from interruption.

Since the shape of a rampart and the form of its terminations are conditioned by the plan of the reef upon which it lies, the rampart at Three Isles follows a smooth curve without such abrupt changes of direction as are associated with the embayment opposite the gap B, and with Asterina Spit and the Shingle Mound on Low Isles.

#### 4. THE BOULDER TRACT.

The difference in the form of the leeward margin of the reef is responsible for a boulder tract of somewhat different character from that of Low Isles. A region containing boulders and fragments occurs, however, where the reef-margin faces a direction between north and west, as at Low Isles.

#### 5. THE REEF FLAT.

This is of the same essential nature as the Low Isles reef flat, but differs from it in some details. It is more extensively covered with water when the tide has ebbed than the flat of Low Isles, but shows a subdivision into regions comparable with the Sand flat and the Thalamita flat. There is no region at Three Isles comparable to the mangrove park at Low Isles, since the mangrove swamp ends on its western side in an almost unbroken wall of trees with no outliers. The moat at Three Isles differs from that at Low Isles in the facts that it is more broken up into sections and has a less flourishing coral fauna.

#### 6. THE ANCHORAGE.

A small inlet with a sandy floor, fringed by reefs supporting a rich growth of coral, and situated to the north-west of the cay, undoubtedly corresponds to the anchorage of Low Isles, although it exists in a reduced form and is differently related to the cay.

Apart from the regions already described, Three Isles possesses the following features which are without exact correspondence at Low Isles.

#### 1. THE DUNE. (Plate XXII, fig. 3.)

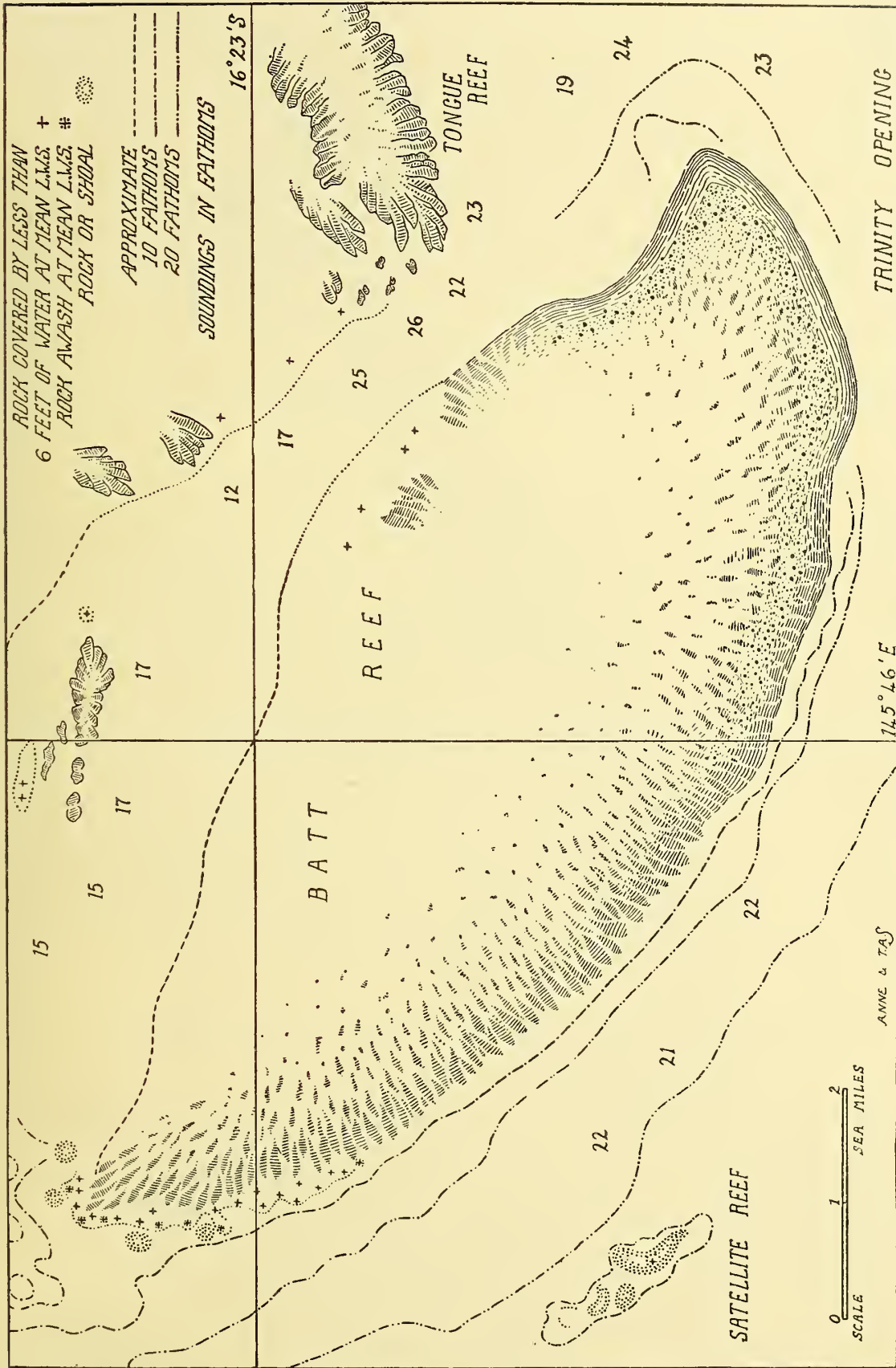
In the south-eastern part of the reef, along the greater part of the seaward edge of the mangrove swamp, there is an accumulation of shingle, sand and pumice forming a dune-like bank about 50 yds. wide and probably as much as 20 ft. above datum at the summit. The inner edge descends steeply into the mangrove swamp, and the district supports a dry-land fauna including characteristic dune plants. At Low Isles nothing of this sort exists, but there is a narrow shingle-ridge in a corresponding position.

#### 2. CASUARINA SPIT.

A spit of clean coral shingle situated at the northern end of the mangrove swamp, and supporting a dry-land flora in which the dominant tree is *Casuarina equisetifolia*.

#### 3. THE THIRD ISLAND. (Text-fig. 14 ; Plate XXII, fig. 2 ; Plate XXVI, fig. 1.)

An area about 900 ft. long and 180 ft. wide, of complex structure. Along its western side runs a platform of hard coral rock. This is much eroded and pot-holed, its seaward edge is cliff-like, and the general level of the surface is such that it is covered at spring tides. East of the rocky platform there is a band of compacted shingle and debris, supporting a flora of grass and bushes, and followed by a ridge of clean shingle. Between this and the flat is a line of *Rhizophora*.



TEXT-FIG. 4.—Batt Reef. This figure is modified from Admiralty Chart no. 2924, and summarizes the knowledge of the reef gained by the Expedition. The representation is purely conventional, since the extent of the pavement indicated by parallel shading round the windward angle of the reef is not known. The unshaded part of the reef represents sand.

## 4. THE PROMENADES.

The seaward margin of the dune leads down to the surface of a platform, in places about 60 ft. wide, of a hard coral rock similar to that of the Third Island. The surface is pitted and pot-holed, and the often precipitous or overhanging outer edge is undercut in places. The platform is subdivided into two somewhat different regions, as follows :

(a) *The High Promenade* (Plate XXII, fig. 1).—In the south-eastern part of its extent, the top of the platform is as much as  $5\frac{1}{2}$  ft. above the level of the low pavement which lies between it and the rampart. There are two interruptions in its course, but its essential continuity for about 1300 ft. justifies its consideration as a separate morphological unit.

(b) *The Low Promenade*.—The northern part of the platform is also more or less interrupted in its course ; it is similar in structure to the high promenade, but considerably lower in level.

Where the margin of the dune overlies the promenades, there is a narrow beach of sand and coral shingle which is continuous, at its northern extremity, with Casuarina Spit.

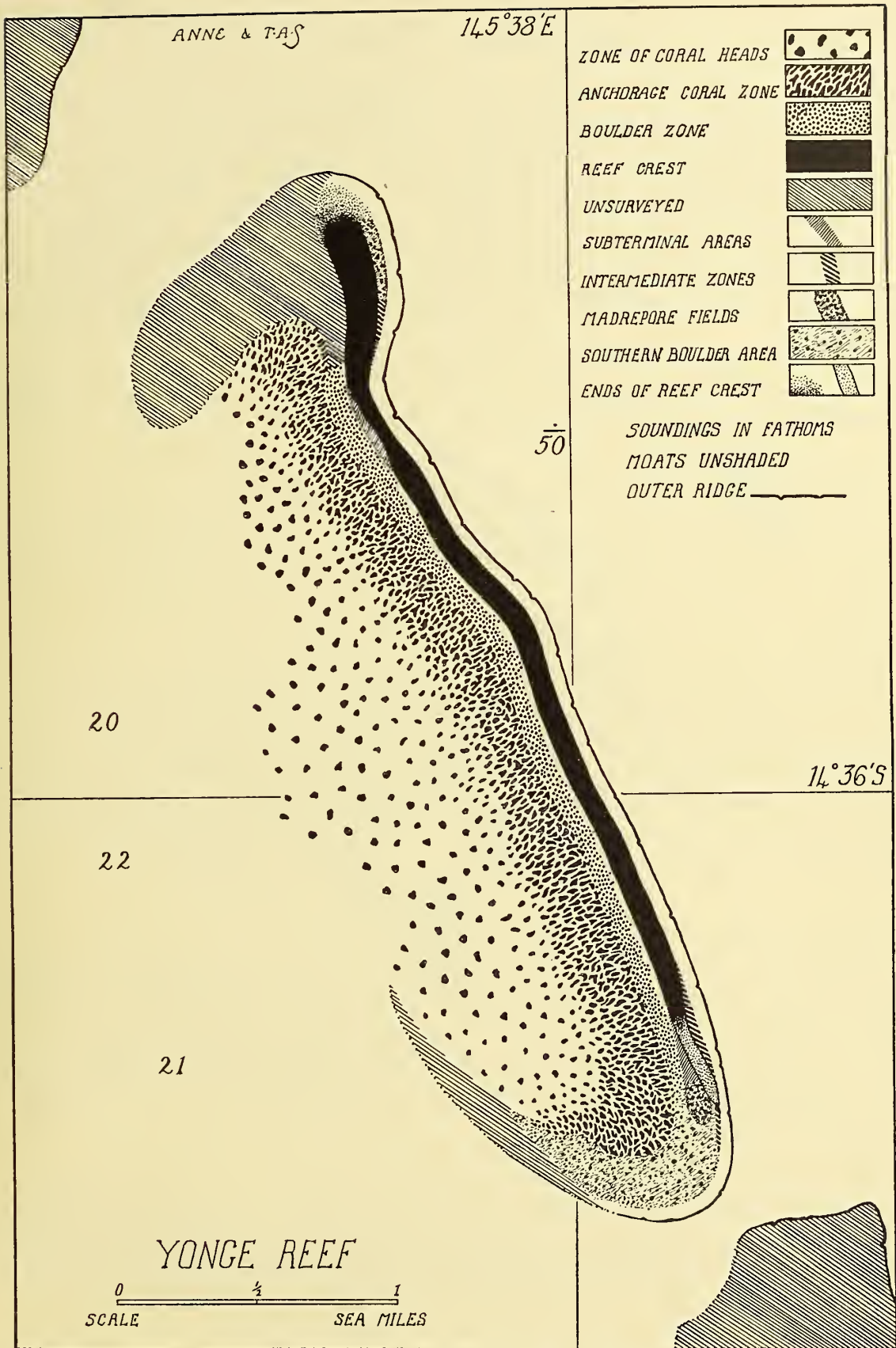
C. BATT REEF. Lat.  $16^{\circ} 23' S.$  (Text-fig. 4 ; Plate XXVI, fig. 2.)

We are unable to give a detailed account of Batt Reef, since it covers an enormous area and is incompletely surveyed, nor were we able to work there sufficiently often. It is about 10 miles long and 4 miles wide, its major axis running about ESE. to WNW. Its north-western corner lies some 7 miles east of Low Isles. The western side of the reef faces the protected sea between Barrier and mainland, and its southern shore flanks Trinity Opening. There is a sharp angle at the south-eastern extremity, and from here northwards until it becomes protected by Tongue Reef the edge is open to the Pacific. Batt Reef has the form of a distorted crescent with its convexity directed south-eastward.

The surface appearance of the central part of Batt Reef is that of a vast sand-flat. At a point visited close to the acute south-eastern extremity the seaward slope consists of a rocky marginal pavement, which passes, without any intervening rampart, into a region closely resembling the Thalamita Flat at Low Isles. There is no deep water inside the arms of the reef, which therefore contains no lagoon but only a central sand-flat. The north-western part of the reef-margin has no rocky boundary, but is much broken up into reef patches. Batt Reef uncovers only at spring tides.

D. YONGE REEF. Lat.  $14^{\circ} 36' S.$  (Text-fig. 5 ; Plate XVII, fig. 2 ;  
Plates XXIII and XXIV ; Plate XXVI, fig. 4.)

Yonge Reef was chosen for careful examination because it appeared from the chart to be a characteristic reef of the Outer Barrier series, and was accessible from a temporary base which we established on Lizard Island. Brief examinations of other reefs (Ribbon Reef, Ruby Reef, Escape Reef), which seemed to be of the same class, confirmed the supposition that although there is considerable variation within the class, Yonge Reef might be regarded as typical. It is a reef quite unlike either of the types which we have hitherto described. It is about 4 miles long, a mile wide, has its major axis directed nearly NNW. to SSE., and is separated from similar reefs in the same series by narrow channels at its northern and southern ends. The reef therefore is of elongate form, and its most



TEXT-FIG. 5.—Diagrammatic representation of Yonge Reef. The size, outline and orientation are taken from Admiralty Chart no. 2923. The relative widths of the zones along the oceanic side were obtained from pacings along a transverse section. The remaining details are sketched in, and the sizes and relations of the small areas near the ends of the reef are very approximate.

solid surface feature, a band-like pavement of rock along its Pacific border, forms a low barrier upon which the energy of the breakers expends itself, their attack being moderated, but rarely ceasing even in calm weather. At the extremities of the reef the margin turns inward towards the mainland, forming two recurving horns, whose course becomes parallel to that of the main body of the reef before they terminate. The area contained within this crescentic margin includes innumerable coral heads and reef-patches, but it is possible to work a boat among them. The reef has no continuous western boundary apart from the recurving horns already described. Its Pacific slope descends rapidly to deep water.

The greater part of the length of the reef (leaving out of account, for the moment, its modified terminal regions) is differentiated into a series of band-like zones, running parallel to one another in the direction of its long axis. The zones have been designated as follows :

1. THE REEF CREST. (Plate XXIII, figs. 1, 3 and 4.)

A pavement of solid coral rock, swept clear of debris, over 3 miles in length and some 160 yds. in breadth. Its general level is slightly higher than that of the surrounding regions, and it constitutes, as it were, the backbone of the reef.

2. THE OUTER MOAT. (Plate XXIII, fig. 1.)

Proceeding from the reef-crest towards the Pacific, one traverses first a moat. The floor of this moat slopes gently downward from the reef-crest to the deepest part, which lies immediately to landward of a second and lower ridge (THE OUTER RIDGE) not far from the breakers. The moat is in many places partly filled up by irregular masses and platforms of coral rock, some of which are continuous with the outer ridge ; but in the main it is well marked, attaining a depth of some 5 ft. in places, close to the outer ridge. Its width is about 100 yds.

3. THE OUTER RIDGE. (Plate XXIII, fig. 2.)

This ridge is not only lower, but also much narrower than the reef-crest. It is fairly continuous, but is interrupted here and there by somewhat wedge-shaped clefts. One may stand upon it at extreme low water, since the breakers curl up and over some few yards to seaward of it. From the ridge it is possible to see that the Pacific slope of the reef is at first gentle, perhaps for a few yards only, with an appearance as of the sudden descent into a chasm beyond.

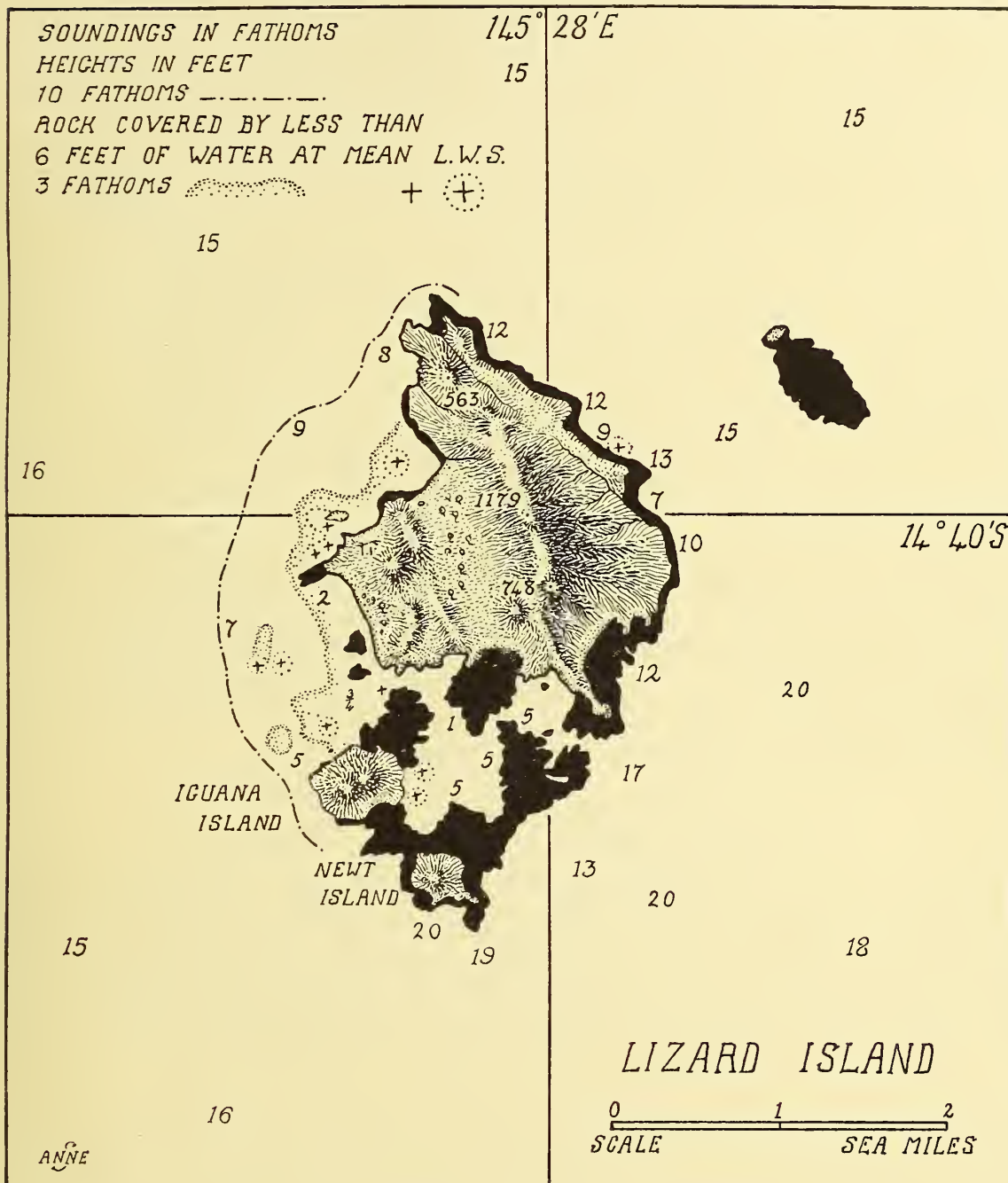
4. THE INNER MOAT. (Plate XXIII, fig. 4.)

A second moat occurs immediately to westward of the reef crest and is about 50 yds. wide. It is less well defined than the outer moat, being intermittent and in places hardly recognizable, but is none the less a distinguishable zone. It is not more than 12 to 18 in. deep, often less.

5. THE BOULDER ZONE.

A belt bounding the inner moat along its western side and composed of boulders, coral fragments and shells, distributed in a haphazard manner.





TEXT-FIG. 6.—Modified from Admiralty Chart no. 2923. The principal reefs, or groups of reef-patches, about the island are represented in solid black. For description see p. 87.

## 6. THE INNER PARTS OF THE REEF. (Plate XXIV.)

From the outer ridge, going westward as far as the boulder zone, there is no large body of water present. Such water as exists is contained within the moats and in pools on the reef-crest and among the boulders. From the western edge of the boulder zone, still going westward, the substratum changes from rock to sand, and the sand is covered by water, continuous with that of the sea between the mainland and the Barrier. At first the sandy floor lies beneath water only a foot or two in depth, but it slopes gradually downward so that before long it has reached a fathom in depth, then 2 or 3 fathoms. By the time the western limit of the reef is reached, between the tips of its recurved horns, the water has become considerably deeper. From this sloping sandy floor there arise masses of coral rock of various forms and sizes, supporting a rich growth of living coral on their upper surfaces. Such of these masses as arise from 2 or 3 fathoms or more, mostly constitute curious table-like structures with precipitous or overhanging sides, and often many feet in diameter. The region in which these occur may be termed the *ZONE OF CORAL HEADS*, and this passes gradually, as the water shallows towards the boulder zone, into the *ANCHORAGE CORAL ZONE*, a region in which the height of the coral masses becomes less and less, and in which they form a labyrinth of intricate reefs with pools and channels between.

As the extremities of Yonge Reef are approached, some of the zones above defined disappear or become modified. The details of these changes are not relevant to the present account, and are described further on in the paper (p. 82). The structure of the recurved horns cannot be described, as we had no opportunity of examining them. Lastly, it should be noted that Yonge Reef is only accessible at low water of the lowest spring tides, and is not uncovered extensively many times in the year. As in the case of Batt Reef, the water floods the exposed parts rapidly after the turn of the tide.

### E. LIZARD ISLAND. Lat. $14^{\circ} 40' S$ . (Text-fig. 6.)

Lizard Island is a granite mountain 1179 ft. high, situated about 15 miles from the mainland, and 10 miles from the Outer Barrier. Upon this island we established a base from which we could visit Yonge Reef. The island is surrounded by fringing-reefs and curious patch-like reefs, unlike any of the types which we have so far described. We were unable to study these in any detail, but a note upon them will be found on p. 87.

## THE ECOLOGY OF LOW ISLES.

(By T. A. and ANNE STEPHENSON and G. TANDY.)

The regions will be treated in the following order :

THE CAY.

THE REEF FLAT.

- A. THE MANGROVE SWAMP.
- B. THE FLAT APART FROM THE SWAMP.
- C. THE MOATS.
- D. THE MANGROVE PARK.
- E. THE ROCKY AREA.
- F. THE THALAMITA FLAT.
- G. THE SANDY AREAS.

THE RAMPARTS AND BOULDER TRACT.

- A. THE OUTER RAMPART.
- B. THE BOULDER TRACT.
- C. THE INNER RAMPART.

THE ANCHORAGE.

THE SEAWARD SLOPES OF THE REEF.

### THE CAY.

(Plate IV, fig. 1 ; Plate V, figs. 1 and 2.)

The Cay itself is of little interest apart from the fact that it supports a dry-land flora and fauna. Its steeply sloping sides are submerged up to the vegetation line at high spring tides, and the most interesting items in their population are burrowing crabs and lamellibranchs. The swiftly running nocturnal crabs *Ocypode ceratophthalma* and *O. cordimana* make numerous burrows in the sand of the slope or on top of the cay ; and in a zone a little above the level of the flat, but well below the vegetation-line, there exists a large population, just beneath the surface, of a small smooth cockle, *Davila plana*.

The top of the Cay varies in level, but is roughly speaking flat. Large areas of it are carpeted by the large-flowered convolvulus *Ipomoea Pes-caprae* (Plate XXI, fig. 1), and this, round the fringe of the flat area in certain parts of its circumference, is associated with other creeping or low-growing plants (*e. g.* *Euphrobia eremophila* and *Vigna marina*), which together constitute a fairly conventional "pes-caprae association" of lesser vegetation. Apart from this ground-flora there are a number of deciduous trees of considerable size (*Terminalia Catappa*), some coconut palms (*Cocos nucifera*), and casuarinas (*C. equisetifolia*), in addition to which there are various bushes of lower growth, conspicuous among them the shiny-leaved evergreen *Scaevola Koenigii*. Climbing plants to be found among the bushes are the white-flowered *Passiflora foetida* and the dodder-like tangles of *Cassytha filiformis*, which latter tend to overgrow heavily the bush upon which they depend. Another notable shrub of more delicate growth is the white Jessamine, *Jasminum*

*simplicifolium*, and other bushes are *Tournefortia argentea*, *Vitex trifolia*, and *Premna obtusifolia*. The continuous occupation of the Cay by lighthouse-keepers for some years must have modified the original flora considerably.

As would be expected, a flora of this description carries with it associated insects and arachnids. The most prolific of these are ants, especially the small reddish-brown species *Pheidole variabilis*, which abounds everywhere. The larger insects are well represented by various grasshoppers (e. g. *Valanga irregularis*), by cockroaches (no doubt imported), beetles, butterflies and moths. The Lepidopteran fauna is considerable, but the majority of the species are night-flying forms attracted by the lighthouse. One species of Danaid butterfly (*Danaida melissa* subspecies *hamata*), a pale blue and black form, was particularly noticeable at certain times when individuals, not in clouds, but as isolated fliers in considerable numbers, would be seen migrating from the mainland, many of them flying past Low Isles and out to sea. The Arachnida are represented by several species of spiders, some of them large, and by small scorpions (*Isometrus maculatus*) belonging to a species which has been introduced with shipping from the oriental region to the tropical and subtropical parts of Asia, Africa and America, as well as of Australia. Sand-flies were sometimes abundant at night on the slopes of the Cay, but there were only occasional mosquitoes. The ordinary "house-fly," *Musca domestica*, was common.

*Beach Sandstone* (Plate V, fig. 2; Plate XIV, fig. 1).—Surrounding the Cay on the lower part of its slopes are the various patches of "beach-rock" or "beach-sandstone," a rock formed by the cementing of the sand of the Cay by the deposition of calcium carbonate between the grains. The six patches of this rock are marked C1-6 on the key chart, and by far the largest of them is C6, the ridged structure of which is illustrated in Plate V, fig. 2. The exposed surfaces of this rock would appear to offer little attraction to organisms, but are extensively colonized none the less by a crust of blue-green algae, by lamellibranchs and gastropods, and to a lesser extent by *Enteromorpha*. The rock is often characterized, however, by the presence of sloping ledges with abrupt or overhanging shoreward margins, and these ledges, together with gullies in the rock and the spaces beneath isolated blocks, provide more protected and shaded crevices in which animals of less hardy disposition may shelter.

Notable amongst the exposed forms of the beach-sandstone is the rock-oyster *Ostrea mordax*, a sharp-edged form of a purplish colour which is gregarious and extremely abundant locally. This species is obliged to tolerate extremely high temperatures, since it inhabits a fairly high level, and is soon exposed by the receding tide, being left high and dry in the scorching sun for a very considerable proportion of its life. A. P. Orr took the temperatures of eight rock-oysters on 7th March, 1929 (not one of the hottest days), and the readings were 38.0°, 39.3°, 40.0°, 40.1°, 41.5°, 41.8°, 44.2°, and 44.8° C. (112.6° F.) respectively, the higher readings being in oysters slightly higher up the shore than the others. These readings are minimal. Still more remarkable is the fact that in the cracks between these oysters there are numerous specimens of a sea anemone (probably a species of *Anthopleura*), which have no protection from the sun beyond mucus and their contained water. *O. mordax* is also interesting in that, no doubt in correlation with its ability to withstand desiccation and high temperatures, it appears to occur principally in a rather strictly defined zone at a high level on the shore. This is well illustrated by fig. 4 on Plate V, where a large boulder is seen to be covered by a cap composed of scores of specimens of *O. mordax*, the lower edge of the cap being sharply

defined by the lower limit to which the oysters extend. The species is by no means restricted to the areas of beach-sandstone, occurring freely elsewhere on the reef wherever a suitable attachment such as a boulder or a mangrove-root is to be found at a proper level.

Noteworthy among the other organisms which inhabit the exposed parts of the sandstone are another oyster (*Chama jukesii*), a small periwinkle (*Planaxis sulcatus*), which occurs in great numbers in hollows and crevices at a high level, and a small species belonging to the Vermetidae. The large chiton *Acanthozostera gemmata* (Plate XXI, fig. 2), which attains a length of 6 in., and is one of the commonest inhabitants of the reef, may also be found exposed on the sand-rock, but this creature typically hides in a crevice as far as possible during the day, coming out freely on to the surface to feed at night. Acorn-barnacles and limpets are also present, but never in the profusion which they attain on many English coasts. Other animals seek the sheltered places habitually.

Two other species worthy of special mention are *Grapsus strigosus* and *Clibanarius virescens*. The former, a swift, long-legged crab with a striped greenish carapace, shelters deep in crevices at low water, but may be seen as the tide leaves or covers the rocks. The latter, a small hermit crab with yellow toes, may be found under detached pieces of rock, where it shelters in companies, some of which contain dozens of specimens, inhabiting shells of the most diverse of small gastropods.

The molluscan fauna of the sandstone, when studied in detail, reveals a succession of species which live in zones one above the other, and beyond these other species which occur without definite arrangement in zones. This zonation will be described in detail by T. Iredale elsewhere in this series of reports. The lower part of the stretch C6 is much attacked by boring lamellibranchs and sipunculids (see also p. 60); these are less prevalent on the small patches of rock to the south of the Cay.

## THE REEF FLAT.

### A. THE MANGROVE SWAMP.

(Plate V, fig. 1; Plate VI, figs. 1 and 2; Plate VII, figs. 1, 3 and 4.)

The several regions included under the general term "mangrove swamp" are diverse in nature and will be described successively; but regarded as a unit, the area has the characteristics of a tidal woodland of well-grown trees, containing glades of several types which are markedly sheltered from the wind and are quiet even on a windy day. The region has been colonized, not only by the dominant mangrove *Rhizophora*, but also by a series of plants and animals characteristic of mangrove swamps or of littoral areas, but not of coral reefs—forms which would normally be found on beaches or in estuaries or low-lying coastal areas on the mainland. Conversely, the swamp is invaded to a certain extent by corals and by other typical reef species.

The regions of the swamp will be considered for descriptive purposes under the following headings:

- The Dense Woodland.
- The Sandy Pools.
- The Passages into the Swamp.
- The Muddy Glades.
- The Shingle Tongues.

THE DENSE WOODLAND. (Plate VII, fig. 3.)

We can say very little about this, because it is of thick growth and almost impenetrable. The trees are nearly all *Rhizophora mucronata*; they grow to a considerable size, their roots and the lower parts of their trunks are submerged at high water, and the ground beneath them consists of mud or muddy sand, often with shallow pools. There are a certain number of epiphytic lichens and fungi on their trunks and branches, and of epizoid sedentary animals on their roots. Snails of the genus *Melarhappe* inhabit their leaves and branches, and crabs, hermits and fishes live among the roots, some of the former climbing the trees. Some of the trees are very old, and some are fine timber-trees with 50 or 60 ft. of clean bole.

THE SANDY POOLS. (Plate VII, fig. 4.)

The largest of these is the pool IM1 of the key chart, which occupies an elongate glade and which does not dry out at low water, but contains even then from a few inches to more than a foot of water. The bottom consists mainly of fairly firm sand, but becomes soft and muddy in places, and is often covered by thin black muddy deposits or by greenish scum. Cyanophyceae are ubiquitous and infest organic debris. Under the roots of mangroves are extensive carpets of the small film-fern-like alga *Caulerpa verticillata*, but the floor is free from *Thalassia*. On the living trees one finds *Melarhappe*, and in the wood of dead ones a flourishing population of *Teredo* of more than one kind. Sponges\* are a feature of the pond, some growing on the ground and others, together with compound ascidians, on mangrove roots, which are also colonized in places by a red-brown *Tubularia*-like hydroid (*Myrionema amboinense*). The fauna of the bottom includes both surface and burrowing species—crabs, hermits, cockles and other bivalves, prawns, tube-making Polychaetes, naticas, etc.† Species of particular interest are the heavy blue and green swimming-crab *Thalamita crenata*, which inhabits part of the mangrove area and also the mangrove park, but only exceptionally strays on to the open flat; the common dingy-coloured mangrove hermit *Clibanarius striolatus*, which abounds in shells of *Pyrazus* and *Telescopium*, and which is also plentiful in the mangrove park, close to the swamp; the cockles *Gafrarium pectinatum* and *G. tumidum*; and the surface-living *Holothuria scabra*.

Other pools somewhat similar to IM1, but much smaller, and offering little of special interest, are IM6 and IM7, the latter having a fairly firm bottom, the former a yielding floor of sand and mud.

There is, however, another small pool of a most interesting nature which may suitably be mentioned here. It lies between the inner rampart and the dense woodland, and is labelled RP3 on the key chart. The bottom here is sand, partly covered by *Thalassia*, and the pond is remarkable for its interesting fauna of coelenterates, clams and holothurians. *Pocillopora bulbosa* flourishes here, sometimes growing on mangrove roots, and other living corals are species of *Acropora*, *Montipora*, *Millepora* and massive *Porites*, and *Astraeids* of more than one genus. *Zoanthids* of two species are common; *Stoichactis kenti* is plentiful, and there is a densely gregarious colony consisting of scores of individuals of the extraordinary sea-anemone *Phyllodiscus cinctus*. This animal stings the fingers

\* The following sponges occur here or in similar places: *Spirastrella purpurea*, *Chalina camerata*, *C. clathrata*, *Cladochalina pulvinatus*, *Gellius toxius*, *G. pumilus* and *Spongelia digitata*.

† The term "natica" is used in this report in a somewhat wide sense, in the same way in which one speaks broadly of "chiton," and covers several species of the genera *Natica* and *Uber*.

quite badly, since in spite of its small size and delicate texture it is well supplied with large nematocysts; it also provides an example of a curious reaction to light. In specimens which were kept alive for a time, the tentacles, which are slender and pale bluish white, were usually kept partially or completely retracted in strong light, whereas the ruff of brown vesicles of complicated structure which occurs halfway down the body was widely expanded. In a dim light the reverse was the case. The clams found in the pool were *Hippopus hippopus*, *Tridacna crocea* and *T. fossor*. Four species of holothurians at least were present, including *H. argus*, *H. leucospilota* and *Synapta maculata*. This pond, together with the passages into the swamp next to be described, offer most curious examples of the presence of elements belonging to the true reef fauna and flora in the marginal and sandy parts of the swamp. The large pond IM1 exhibits this also, but in a lesser degree.

#### THE PASSAGES INTO THE SWAMP.

These passages deserve special mention, since they illustrate further the penetration of reef-animals into the woodland which has just been noted. The most perfectly developed of these passages are striking and curious features, consisting of a number of narrow, regular tunnels, free from trees and floored in the main by sand, which lead from the mangrove park into the pools inside the swamp. The adjacent tunnels P5-7 may be described as examples. Of these P5 is the most perfect, P6 nearly as well defined, P7 imperfect. They are channels, deep in parts, with a firm sandy floor grading locally into mud. In the entrances from the park there is *Thalassia* and *Halimeda*, and *Caulerpa verticillata* on or under mangrove roots. The water in the passages is inhabited by a small garfish, *Zenarchopterus dispar*, a species new to the Australian fauna. On roots flanking the passages, and on shells and dead coral among them, are small living colonies of massive *Porites* and *Cyphastrea*, of a species of *Leptastrea* and a peculiar species of *Porites*, the last especially being common. The most striking feature lies in the sponges, which are numerous and of several kinds. Compound Ascidians are also common, many of these and the sponges, together with oysters, living on roots. The Ascidians include a small pink species of *Didemnum* and the green *Diplosoma virens*. Noteworthy among the sponges is *Gellius toxius*, a soft, purplish-black form which trails along the roots and which has tall chimney-like tubes bearing the oscula. *Melarhaphé* and hermits, as usual, climb the trees. Conditions of life in these passages are affected by a distinct scour of water through them during the ebb and flow of the tide. A. P. Orr states that in one of the passages where he worked, except at slack water of high tides, there is a current of up to about 3 miles per hour or more.

#### THE MUDDY GLADES. (Plate VI, figs. 1 and 2; Plate XXVII.)

These are sinister places which might be a hundred miles from any coral reef for all the connection they appear to have with it. They are openings in the trees, floored by foul black mud on which lie whelks of unpleasant aspect by the score, amid dead tree-trunks riddled by *Teredo*; their floors are exposed at low water, leaving only shallow pools here and there. The fauna is distinctive. The whelks (Plate VI, fig. 2), black creatures with dingy pyramidal shells, are *Telescopium telescopium* and *Pyrazus palustris*. These form one of the most marked characteristics of the mud-glades, although

they occur elsewhere in the swamp. Their shells are common in the sandy pools and peripheral regions, but are there usually tenanted by *Clibanarius striolatus*. Another abundant inhabitant of the mud-glades is the skipping fish *Periophthalmus koelreuteri*, in addition to which are the burrowing red Crustacean *Thalassina anomala*, numerous crabs which also burrow in the mud, and small gastropods. The large black lamellibranch, *Cyrena coaxans*, is also to be found (this being sometimes used for food by native crews, if one may judge from the existence of a pile of empty shells on one of the shingle tongues), and even in this black mud there are naticas. On the shells of *Telescopium* and *Pyrasus* may be found oysters (e. g. *O. mordax*). The black mud, although one sinks into it knee-deep, is actually a superficial layer, as has been demonstrated by the boring described in another report by A. P. Orr (Vol. I, No. 5, p. 117); the mud appears to be *superimposed upon the reef flat*. The glades above described are those marked IM2, IM4 and IM5 on the key chart. They vary a little individually, but the description given applies in general to all of them. The mangrove *Bruguiera Rheedii* occurs in places along their margins.

#### THE SHINGLE TONGUES. (Plate VII, fig. 1; Plate XXVII.)

These are regions of coral shingle inside the mangrove area, which are covered for the most part at high water of tides rising about 7 ft. above datum. So far as we can judge, they appear to antedate the mangroves. As the two tongues are rather different, they will be described separately.

IM4B is a large L-shaped area of shingle, which is limited on its seaward side by the inner rampart, and flanked along the greater part of its other edges by the mud-glades IM4 and IM5. It forms dry land at low water, and consists of dirty shingle, loose on top, but fairly compact and mixed with sand and mud below. In places the shingle is much infested by blackish rust-like Cyanophyceae, and supports patches of the fleshy creeping plant *Sesuvium Portulacastrum* (a form reminiscent of *Mesembryanthemum*, Plate XIX, fig. 3), and in addition to this a grass and other low-growing plants. The fauna is interesting, consisting of isopods (probably of more than one species, including *Ligia australiensis*), some of which move extremely rapidly; of small scuttling crabs; of numerous small gastropods of several kinds, many of them under the shingle; of black and green ants (including *Oecophylla smaragdina* subspecies *virescens*, and *Polyrhachis sokolova*), and of butterflies, sand-flies and other small flies. There are also geckos and, perhaps most curious of all, earthworms (*Pontodrilus bermudensis*) are to be found in the mud beneath the shingle. This area is also characterized by the presence of a number of enormous pits, a foot or more in diameter, excavated in the shingle by the large blue mangrove crab *Scylla serrata*. At the bottom of the pit, which is inclined at an angle, there is sometimes standing water, in which the crab may be seen. At Low Isles these burrows occur mostly on this one spot, but are found occasionally on the Long Tongue and the inner rampart. This habit of digging in shingle is apparently an exceptional one for the species, which is a well-known mangrove crab of the Australian coast, but normally burrows in mud.

On the surface of this shingle area there are two small banks higher in level than the rest (Green Ant Island and IM4A), which must constitute dry land even at high water, at ordinary tides. Green Ant Island (Plate VII, fig. 1) is a remarkable spot, composed of fine-grained clean shingle and sand, contrasting sharply with the coarse, dirty shingle of the greater part of the tongue, and supporting a dense thicket of characteristic dry-land scrub, of the type which colonizes a mainland strand. The flora of flowering plants on



these few square yards is considerable, and notable among them are the tree *Thespesia populnea*, the scandent *Flagellaria indica*, the blue-flowering herb *Commelina cyanea*, the grass *Lepturus repens*, and *Achyranthes aspera*. These species most of them occur on Green Ant Island only. The green ant, *Oecophylla smaragdina*, swarms all over this vegetation. The mound IM4A is similar to Green Ant Island, but its flora contains fewer species, among which are *Thespesia populnea* and the Milky Mangrove *Excoecaria agallocha*.

The other shingle area, the Long Tongue of the chart, is an elongated ridge considerably overgrown by trees, and merging at its edges into dense woodland on one side, and into the mud-glade IM2 on the other. At its northern extremity it meets an area consisting of patches of soft muddy gravel grading into swamp, but the ridge proper constitutes, at low water, a corridor of firm land through the trees, made of coral shingle knit together by sand and mud. The soft northern area is honeycombed by the burrows of various crabs, notably *Gelasimus dussumieri*, the males of which have one enormously developed chela, and are brilliantly coloured in cobalt blue, white and orange, whilst the females lack the large claw and are dark greenish in colour. The mangrove whelks occur in this region. The dry part of the tongue also contains many crab-burrows, and has a fauna of black and green ants, small gastropods, isopods and earthworms, as in the case of IM4B. At one side of the tongue is a small area of fine white shingle, *Sesuvium* and bushes, similar to IM4A. The large brilliant green and black butterfly *Troides priamus* subspecies *euphorion* was seen in this region. Organisms characteristic of the shingle-tongues (though not necessarily confined to them) are indicated by asterisks in the list on p. 42.

#### ANALYSIS OF THE FAUNA AND FLORA OF THE MANGROVE AREA.

The fauna and flora of the mangrove area as a whole, therefore, include several types of plant and animal community. The species overrun each other's territory to a certain extent, but the distinction into groups is none the less apparent. The fauna and flora may be analysed as follows :—

##### I. The principal animal communities are three in number :

1. The characteristic inhabitants of the muddy glades.
2. Those of the shingle tongues, which include dry-land and littoral forms.
3. Those of the sandy pools and passages, where reef and mangrove fauna intermingle, but where only certain members of the reef fauna penetrate.

##### II. The flora is differentiated into three series :

1. *Rhizophora* and its associates.
2. *Sesuvium* and other low-growing forms.
3. A dry-land flora, including species which may occur elsewhere in situations unconnected with shore or mangroves, sometimes at high levels.

##### III. The following points are also relevant :

1. The mangrove area includes species which are limited to it or which do not stray far beyond it. Such are *Pyrazus*, *Telescopium*, *Thalassina*, *Scylla*, *Clibanarius striolatus* and *Periophthalmus*.
2. It includes also, particularly on the shingle tongues, species which may occur on the mainland apart from mangrove areas—*e. g.* ants, geckos, flowering plants, earthworms, and some of the gastropods. Even *Periophthalmus* is sometimes a littoral form unconnected with mangroves.

3. Forms such as *Metopograpsus messor* are equally characteristic of the mangrove area and the ramparts. Crabs of the genus *Gelasimus* are plentiful in certain places outside the swamp as well as inside it.
4. The list given below does not include the corals, sponges, ascidians, holothurians, hydroids and anemones, which clearly belong to the reef-fauna proper.

The Low Isles mangrove area, therefore, shelters a number of forms, whether littoral or palustrine, which would not occur on a coral reef pure and simple—that is to say, on one such as Batt Reef or a member of the Outer Barrier series, where nothing is exposed at high water. Many of the swamp animals are species modified for aerial respiration, and some of the plants have accessory breathing organs connected with the immersion of their roots in mud.

#### SPECIES CHARACTERISTIC OF THE MANGROVE AREA.

(Asterisks indicate organisms characteristic of the shingle tongues, though not necessarily confined to them.)

#### ANIMALS.

##### OLIGOCHAETA.

\**Pontodrilus bermudensis*.

##### ISOPODA.

\**Ligia australiensis*.

##### ANOMURA.

*Thalassina anomala*.

*Clibanarius striolatus*.

##### BRACHYURA.

\**Scylla serrata*.

*Thalamita crenata*.

*Sesarma bidens*.

„ *villosa*.

*Euplax tridentatus*.

\**Metopograpsus messor*.

*Gelasimus annulipes*.

„ *dussumieri*.

##### INSECTA.

\**Oecophyllia smaragdina*.

\**Polyrhachis sokolova*.

Sand-flies and mosquitoes.

##### GASTROPODA.

*Nerita lineata*.

„ *planospira*.

\* „ *plicata*.

\* „ *striata*.

##### GASTROPODA—*continued*.

\**Bembicium melanostoma*.

\**Melarhappe scabra*.

\* „ *undulata*.

*Pythia nux*.

\**Melampus adamsianus*.

\* „ *granifer*.

\**Quoyia decollata*.

*Pyrazus palustris*.

*Telescopium telescopium*.

\**Cerithium patulum*.

*Naticidae*.

##### LAMELLIBRANCHIA.

*Ostrea mordax*.

*Gafrarium pectinatum*.

„ *tumidum*.

*Tellina palatam*.

„ *remies*.

*Cyrena coaxans*.

*Teredo*.

##### PISCES.

*Periophthalmus koelreuteri*.

var. *argentilineatus*.

##### REPTILIA.

\**Geckos*.

#### PLANTS.

##### PHANEROGAMS.

\**Commelina cyanea*.

\**Achyranthes aspera*.

\**Lepturus repens*.

\**Excoecaria agallocha*.

\**Avicennia officinalis*.

\**Thespesia populnea*.

*Rhizophora mucronata*.

*Bruguiera Rheedii*.

##### PHANEROGAMS—*continued*.

*Ceriops tagal*.

\**Sesuvium Portulacastrum*.

\**Flagellaria indica*.

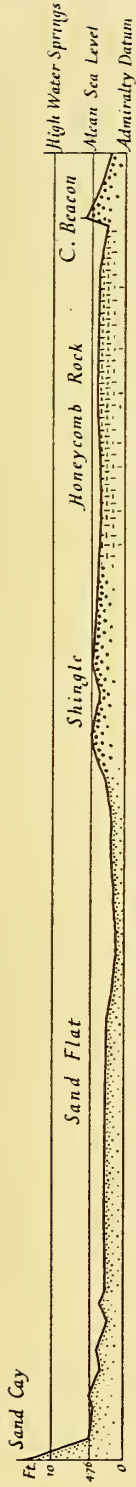
##### CRYPTOGAMS.

*Caulerpa verticillata*.

\**Cyanophyceae*.

Lichens.

Fungi.



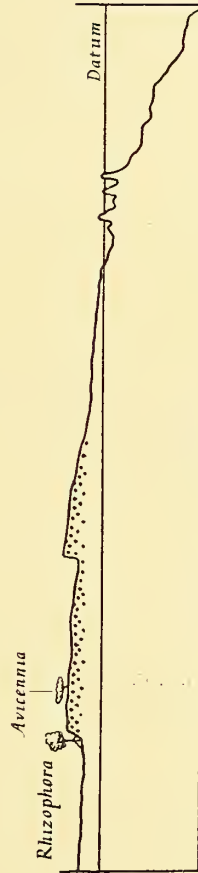
Section from Cay to C. Beacon Vertical exaggeration 20 times

8



Section from C. Beacon to B. Beacon Vertical exaggeration 20 times

7



Vertical scale exaggerated 7 1/2 times

3

TEXT-FIG. 7.—Sections across the Low Isles flat, and across the ramparts. The positions of these sections on the reef are indicated in Text-fig. 11. Note the difference in height between the eastern part of the flat (about 4 ft. above datum) and of the western part (2.2 to 2.5 ft.); section 9 in Text-fig. 11 (not illustrated here) amplifies the information represented here, giving heights of 2.5–3.2 ft. across the flat. The number beside each section corresponds to a number in Text-fig. 11.

## B. THE FLAT APART FROM THE SWAMP.

It will be advisable before describing the several parts in detail to consider the reef-flat in general, as distinct from the mangrove area, which forms a very special part of it.

The following is a list of organisms which may be regarded as typical reef-flat species. If we consider the flat as comprising three principal regions—the moats, the mangrove park, and the western part (including Thalamita flat, Sand flat, and adjacent areas)—the great majority of these organisms occur in all three regions. This does not mean that some of them are not more abundant on one part of the flat than another, nor that given species are not specially characteristic of particular areas; but it provides an indication of the range of life on the flat, on the basis of which the differentiations may afterwards be considered. Sand-dwelling animals are listed separately on p. 56.

## SPECIES CHARACTERISTIC OF THE REEF FLAT.

## ANIMALS.

- |                               |                         |
|-------------------------------|-------------------------|
| FORAMINIFERA.                 | CIRRIPEDIA.             |
| Orbitolites complanata.       | Acorn barnacles.        |
| PORIFERA.                     | NATANTIA.               |
| Cinachyra australiensis.      | Crangon strenuus.       |
| Gellius fibulatus.            | „ ventrosus.            |
| „ sagittarius.                | ANOMURA.                |
| Clathria aculeata.            | Clibanarius virescens.  |
| Spirastrella purpurea.        | Dardanus megistos.      |
| Euspongia irregularis.        | BRACHYURA.              |
| var. pertusa.                 | Calappa hepatica.       |
| HYDROZOA.                     | Thalamita admete.       |
| Myrionema amboinense.         | „ stimpsonii.           |
| Dynamena crisioides.          | Actaea hirsutimana.     |
| ZOANTHINARIA.                 | Atergatis ocyroe.       |
| More than one common species. | Phymodius ungulatus.    |
| ACTINIARIA.                   | Pilumnus vespertilio.   |
| Stoichactis kenti.            | STOMATOPODA.            |
| Actinodendron plumosum.       | Gonodactylus chiragra.  |
| MADREPORARIA.                 | AMPHINEURA.             |
| Pocillopora bulbosa.          | Schizochiton incisus.   |
| Leptastrea.                   | Acanthozostera gemmata. |
| Galaxea.                      | GASTROPODA.             |
| Favia.                        | Trochus fenestratus.    |
| Montipora ramosa.             | „ niloticus.            |
| Acropora hebes.               | Vermetidae.             |
| Porites (massive forms).      | Cypraea annulus.        |
| POLYCHAETA.                   | „ errones.              |
| Eurythoe complanata.          | „ moneta.               |
| Iphione muricata.             | Strombus luhuanus.      |
| Spirobranchus giganteus.      | Pterocera crocata.      |
| SIPUNCULOIDEA.                | Melo diadema.           |
| Boring species.               | Siphonaria denticulata. |
|                               | Onchidium.              |

ANIMALS—*continued.*

## LAMELLIBRANCHIA.

- Ostrea cerata.  
 „ crista-galli.  
 „ mordax.  
 Spondylus ducalis.  
 Lima tenera.  
 Pinctada margaritifera.  
 Isognoma isognomum.  
 Modiolus auriculatus.  
 Boring species (Lithophaga, etc.).  
 Arca fusca.  
 Tridacna crocea.  
 „ fossor.  
 Hippopus hippopus.  
 Chama jukesii.

## ASTEROIDEA.

- Linckia laevigata.  
 Nardoa pauciforis.  
 Culcita novae-guineae.

## ECHINOIDEA.

- Echinometra mathaei.  
 Tripneustes gratilla.  
 Centrechinus setosus.

## OPHIUROIDEA.

- Ophiothrix longipeda.  
 Ophiocoma scolopendrina.  
 Ophiarthrum elegans.

## HOLOTHUROIDEA.

- Synapta maculata.  
 Stichopus chloronotus.  
 Holothuria atra.  
 „ coluber.  
 „ leucospilota.

## ASCIDIACEA.

- Didemnum candidum.  
 Diplosoma virens.

## PLANTS.

## PHANEROGAMS.

- Rhizophora mucronata.  
 Halophila ovalis.  
 Thalassia Hemprichii.

## PHAEOPHYCEAE.

- Sargassum lanceolatum.  
 „ latifolium.  
 „ torvum.  
 Turbinaria turbinata.  
 Hydroclathrus clathratus.  
 Cystophyllum muricatum.  
 Dictyota Bartayresiana.  
 „ ciliata.  
 Padina australis.  
 „ Commersonii.

## CHLOROPHYCEAE.

- Caulerpa peltata.  
 „ racemosa.  
 Halimeda cuneata.  
 „ Opuntia.

CHLOROPHYCEAE—*continued.*

- Bornetella nitida.  
 Dictyosphaeria favulosa.  
 „ sericea.  
 „ Versluysii.  
 Boodlea paradoxa.

## FLORIDEAE.

- Laurencia botryoides.  
 „ papillosa.  
 Acanthophora spicifera.  
 Spyridia filamentosa.  
 Digenea simplex.  
 Amphiroa fragilissima.  
 Melobesieae (encrusting forms).

## CYANOPHYCEAE.

- Species of the group very prevalent,  
 including—  
 Lyngbya majuscula and  
 Hormothamnium solutum.

## c. THE MOATS. (Plate VIII, figs. 2 and 3 ; Plate IX, figs. 1, 3 and 4, etc.)

## CONDITIONS OF LIFE IN THE MOATS.

The conditions which prevail in the moats are clearly of a special nature, and will determine somewhat strictly the range of life which can flourish there. Any organism attempting to establish itself will be subject to the following circumstances :

1. The water is shallow, and is still during much of the period of low water.

2. The temperature during this time therefore becomes very high in hot, calm weather, and may exceed 35° C. (95° F.), though probably rarely, if ever, reaching 40° C.

3. The organisms not living in protected positions are exposed to very strong illumination.

4. During the wet season a heavy fall of rain during the period of low water may cause a sudden change of salinity, which will not be rectified until the tide covers the flat. We can record a range only of 35‰ to 27‰; but undoubtedly the salinity sometimes falls considerably lower than 27‰; for a pool 12 cm. deep with little growing coral, we have a record of 17.1‰.

5. During the ebb and flow of the tide a distinct series of currents is set up in the moats, since the water drains away through the gaps in the rampart and boulder tract, after the main volume of it has left the flat, and enters again through these before it submerges the flat as a whole.

6. A considerable to-and-fro movement of sediment appears to take place in the moats as a result of the currents just mentioned. The actual amount of fresh deposition taking place is probably low.

7. At the end of the period of low water, during the daytime, the oxygen-saturation of the water is very high, and may reach 270%. At the end of low water at night, however, it may fall as low as 20%, and in the event of an occurrence such as a serious visitation of *Trichodesmium*, the oxygen-content may become reduced to zero or very near it, even during the day.

Conditions of life on other parts of the flat will represent modifications of this state of affairs, varying according to situation, nature of substratum and depth of the pools isolated at low water.

#### THE WESTERN, MIDDLE, FUNGIA AND MADREPORE MOATS.

This principal stretch of moat is above all that region of the flat in which coral growth predominates. It is a continuous pool of winding form, lying just inside the western part of the rampart and boulder tract; it is a foot deep or rather more in its deeper parts, and gradually becomes shallower towards the Thalamita flat. This shallow side, indeed, is often rather distinct from the rest, since long trailers of bladder-wrack (*Cystophyllum* and *Sargassum*) are plentiful here, and the growth of branching corals relatively sparse.

*Coral Platforms* (Plate VIII, figs. 3 and 4; Plate IX, fig. 1).—In the seaward part, however, *Montipora ramosa*, *Acropora hebes* and massive *Porites* are in the ascendant, and between them occupy a high proportion of the available space. These corals exhibit a curious development connected with the shallowness of the water. They grow in a normal fashion until their tops project above the level of low water; they may then survive with projecting tips for a longer or shorter period; but sooner or later the projecting parts are killed, become infested by microphytic algae and sediment, and encrusted by nullipores (*Melobesiae*)\*; so that ultimately the coral colonies are converted into flat-topped platforms, dead across the top and alive around the edges. This process may affect individual colonies or, if the growth has been dense so that fields of branching colonies have been formed, it may convert a whole field into a platform. The general

\* The group of calcareous algae which includes *Lithothamnion* and related genera.

result of this is to create a bewildering maze of level platforms with pools between. Three of our figures illustrate this process. In Plate IX, fig. 1, may be seen (on the left) a tuft of *Montipora ramosa* which is as yet alive on top; to the right is another tuft in which the death and flattening of the top has begun. Plate X, fig. 4, gives a detailed view of the top of a platform in an advanced stage of formation, and shows the overgrowth of nullipores and the general incrustation of the surface. Plate VIII, fig. 3, shows the general appearance of the moat close to the gap C, where *Acropora hebes* predominates; and in this case the platforms are not yet dead on the top. The extent and composition of the platforms varies in different parts of the moat; massive *Porites* becomes converted into platforms as readily as the branched species, though the details are a little different. Astraeid corals, especially species of *Favia*,\* are common among the platform-building forms (Plate IX, figs. 3 and 4), and these also often develop dead flattened tops.

*Inhabitants of the Platforms* (Plate X, figs. 1, 3 and 4).—The interstices of the coral platforms offer a home to innumerable commensal, boring and shelter-loving forms of life, the more or less concealed fauna and flora being rich in species as well as in individuals. The urchin *Echinometra mathaei* (Plate X, fig. 3) is common, and there are anemones of a number of species, besides various crabs and prawns. Nullipores are usually well developed and richly coloured on shaded surfaces.

The commensal crabs, prawns and fishes which are found on living coral and anemones may suitably be mentioned here, since they are abundant in the moats as well as in certain other places. Several of the common anemones harbour fish, prawns or both; we have not seen these commensals enter the coelenteron of the polyp, but they shelter freely among the tentacles. Commensal fish and crustacea are widespread among the living coral, different species of coral often having particular commensals, which are usually so coloured that they tone with the coral or contrast suitably with it. A dull reddish madreporic, for instance, may shelter a colony of small fish, sometimes brilliant green in colour, sometimes bright yellow. One of the dominant corals of the moats is *Pocillopora bulbosa*, a yellowish brown branching form which commonly shelters the red and purplish crab *Trapezia cymodoce*.†

*General Population of the Moats* (Plate IX, figs. 3 and 4; Plates X, fig. 2; Plate XVIII, figs. 1-4; Plate XX, fig. 2).—Among the platforms and in the pools between them are to be found a number of other animals, and among these the clams are important. The Low Isles moat supported several specimens of the giant species *Tridacna derasa* (Plate XVIII, fig. 2). The smaller species, *T. crocea* and *T. fossor* are very abundant, and these are extremely conspicuous because of the extraordinary range of brilliant colours and patterns exhibited by the exposed edges of their mantles.

\* The generic name *Favia* is used in this report in a broad sense, as covering the species sometimes grouped under *Favia*, *Favites*, *Acanthastrca* and *Goniastrea*. It is a matter for discussion whether or no these groups should be regarded as valid genera, but for ecological purposes they may be suitably included under *Favia*.

† Some further details are as follows: Less common commensals of *Pocillopora bulbosa* are the crabs *Actaea polyacanthu* and *Cymo andreossi*, and a species of *Periclimenes* (a prawn). The large anemone *Stoichactis kenti* and the crevice-dwelling anemone *Thalassianthus hypnoides* often shelter the prawn *Periclimenes brevicarpalis*. A similar if not identical prawn lives with the actinians *Actinodendron plumosum*, *Cryptodendron adhaesivum*, and *Thalassianthus hemprichii*. *S. kenti* often provides a home for small fish, *Amphiprion bicinctus* and *Actinicola percula*. Some crevice-haunting species of the platforms are the crabs *Atergatis ocyroe* (very common), *Eriphia sebana* and *Pilumnus spinicarpus*: the prawn *Periclimenes spiniferus*; and soft corals of the genera *Rhodactis* and *Actinotryx*.

The colours range from deep peacock blue or violet, through a variety of shades of brilliant green and paler blue to purple and gold, brown and yellow, and so forth. In the case of *T. fossor* almost any pattern imaginable may be found in one specimen or another; but in spite of this variability, it does not produce quite the same series of patterns as do the other species mentioned. Another very common clam, *Hippopus hippopus*, introduces variations upon a duller set of colours; and the rarer *T. squamosa* produces yet another kind of pattern. Two mantles with completely different patterns, though probably both belonging to the same species, are illustrated in Plate XVIII, figs. 3 and 4; and other examples, from different species, may be seen in Plate XVIII, figs. 1 and 2.

Echinoderms are a feature of the moat, among them the brilliant blue starfish *Linckia laevigata* (Plate X, fig. 2), and the holothurians *Stichopus chloronotus*, *Holothuria leucospilota* and *H. coluber*. Isolated individuals of the long-spined urchin *Centrochinus (Diadema) setosis* are fairly common, and sometimes colonies of them (Plate XX, fig. 2) are found, which may remain in approximately the same situation for months at a time. A straggling branched sponge, green in colour, is of frequent occurrence and rapid growth; this form is actually a combination of a sponge (*Gellius fibulatus*) with an alga. Another sponge, bright magenta in colour (*G. sagittarius*), is conspicuous, at least at certain times of year; it has curious flower-like crowns, which frequently become detached and float away on the water. The living coral, especially the massive forms of *Porites*, is much colonized by the tube-dwelling polychaete *Spirobranchus giganteus*, which expands fans of deep blue, scarlet, and other colours at the surface.

The algae of the moats are abundant. Some of them make turf-like tangles amongst the platforms, often overgrowing the coral to a considerable extent, or carpeting areas of dead rocky substratum. These forms include the bright green sponge-like masses of *Boodleia paradoxa*, and several species of "red" algae, which in this case are usually brownish or yellow-green in colour.\* Apart from forms of low or mossy growth, there are several characteristic species of brown algae which attain a larger size. *Turbinaria turbinata* is one of these, and this species is a typical moat-dwelling form, whereas *T. ornata*, which is plentiful outside the rampart, is relatively infrequent inside it. The tufts of *Padina australis* and *P. Commersonii* are ubiquitous, neither species being restricted, apparently, to a particular habitat. The calcareous alga *Halimeda opuntia* is plentiful in the platforms; *H. cuneata*, which is less common, appears to prefer bare sand. Species of *Caulerpa* creep over coral blocks, and species of *Dictyosphaeria* are common on surfaces where they are exposed to very strong illumination and become bleached and powdery-looking in consequence.

The shells of clams, especially those of *Hippopus*, offer a foundation for a complicated fauna and flora of their own, and are extensively bored into from outside by various organisms, including a filamentous alga which makes the inside of the shell green.

The sandy floor of the moat is rarely free from *Thalassia Hemprichii*, but this is usually of relatively sparse growth and does not form a dense turf like that of the mangrove park. Its leaves, here as elsewhere, may be heavily colonized by epiphytes and epizoa.† Occasional seedlings of *Rhizophora* take root in the moats, but do not survive.

\* *Acanthophora spicifera*, *Digenea simplex*, *Laurencia papillosa*, *L. botryoides*, etc.

† The epiphytes of *Thalassia* include species of *Ectocarpus* and *Polysiphonia*. *Valonia Forbesii* is a common epiphyte of the red alga *Digenea simplex*. Frequent epizoa are the ascidian *Diplosoma virens* and the foraminiferan *Orbitolites complanata*.



## INDIVIDUAL CHARACTERISTICS OF PARTICULAR MOATS.

(1) *The Western Moat*.—The special feature here is that a very considerable number of coral species are represented, although many of them must be regarded rather as occasional intruders which have managed to survive, than as forms which are really suited to the locality. Beyond the species already mentioned, certain others are fairly common, and the total number of genera represented is at least fifteen.

(2) *The Middle Moat*.—That part of the Middle and Western moats which lies next to Asterina spit is largely occupied by a rocky platform, partly exposed at low water, on which the turf of *Boodlea*, *Hydroclathrus* and other algae is particularly well developed, and in parts of which the coral *Psammocora* is common. This latter form is almost confined, on the flat, to several regions near Asterina spit.

(3) *The Fungia Moat*.—This was named "Fungia moat" because it was characterized by the presence, amongst the dead branched coral which chokes up a good deal of it, of a large colony of *Fungia*. Three species at least were represented, of which one (a small night-flowering form) was very common, a much larger one which expands its tentacles during the day being less plentiful. The attached young of these species, in various stages of development, were abundant in the shelter of the dead coral.

(4) *The Madrepora Moat*.—A stretch containing a very healthy growth of coral, but of rather fewer species than in other parts.

(5) *The Northern and North-East Moats*.—These represent somewhat pale reflections of the principal moats already described. In the Northern moat species of *Galaxaura* are abundant, and there is a certain amount of immigration of animal species from the Anchorage. A small patch of the grass-like *Diplanthera uninervis*, found nowhere else on the reef, occurred here. In certain runnels (between Clam Spit and the Cay; between Tripneustes Spit and the Shingle Mound) there was a turf consisting of an almost pure growth of *Hydroclathrus clathratus*. This began to disappear in February, 1929. In the north-east moat the coralline *Amphiroa fragilissima*, which is ubiquitous in the moats, attains an abundance not paralleled elsewhere.

(6) *The Discontinuous Moat-pools*.—The series of discontinuous pools which lie inside the escarpment of the outer rampart, starting at the pool M1 of the key chart, and going round in an anti-clockwise direction as far as the pool M13, have been classed as a matter of convenience with the moats. They are, however, of a rather different nature. The large pool M7 is distinguished from the rest of the series because it has an arm which penetrates the mangrove swamp. It has a fairly typical moat population, and is peculiar in the possession of a special richness of *Stoichactis kenti*, of small Zoanthids which in places form a yielding carpet yards in extent, and in the existence of a few healthy colonies of fleshy alcyonaria (which occur here and there in moats, but are not among the characteristic forms) close to the mangroves. It includes also organisms characteristic of the mangrove park (e.g. *Myrionema amboinense*), and at the northern and southern ends of its seaward portion resembles the other pools in the series. Apart from this pool, the others have a more or less rocky floor, which, in the more western ones consists partly of honeycomb-rock (see p. 52 and Text-fig. 8), in the more easterly of inner rampart material. These pools vary individually, but are shallow and contain little or no living coral, the most noteworthy organisms being *Hippopus*, *Gellius fibulatus*, *Ophiocoma scolopendrina*,

*Cypraea annulus*, holothurians (*H. atra*, *H. leucospilota*, etc.), *Pilumnus vespertilio*, *Onchidium*, *Stoichactis kenti*, and turfs of algae (*Dictyosphaeria*, *Laurencia*, *Caulerpa*, *Halimeda*, etc.).

(7) *Porites Pond*.—The pool thus labelled on the chart is an isolated piece of moat of considerable depth in its northern and western part, shallowing to eastward and southward. It has a flourishing population of coral, amongst which massive *Porites* of large size is dominant; and supports a typical population of moat animals.

#### D. THE MANGROVE PARK.

(Plate VII, fig. 2; Plate XIII, fig. 4; Plate XIX, fig. 1.)

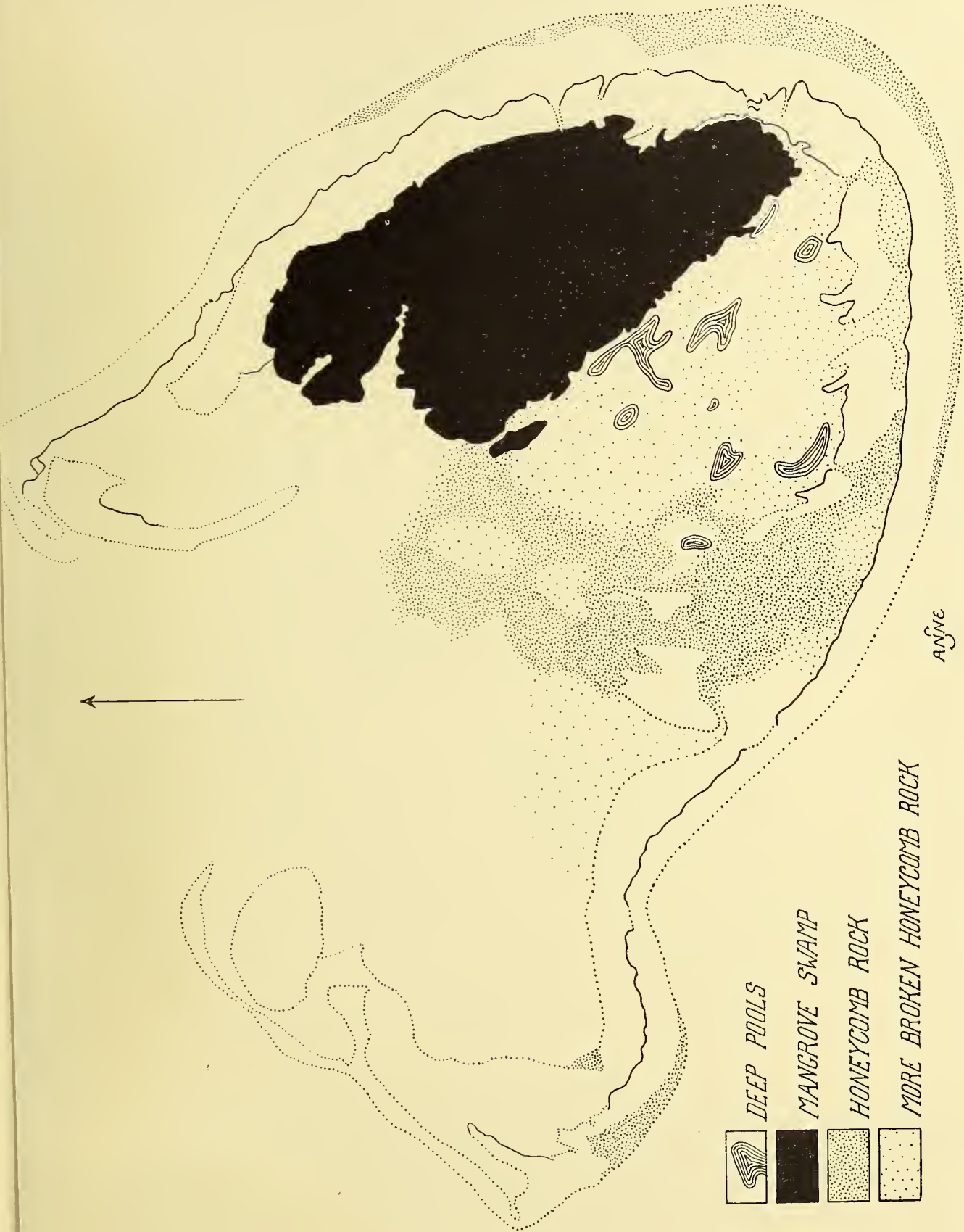
The mangrove park covers a large area, and its floor varies considerably both in nature and in level from one part to another. The "park" comprises approximately that part of the flat which is more or less successfully colonized by outlying trees or saplings of *Rhizophora mucronata* with their remarkably developed stilt-roots. Some idea of its nature may be gained from Plate XIII, fig. 4, but one cannot show in a photograph the other feature which characterizes the region, the greensward beneath the water due to the rich growth of *Thalassia Hemprichii*. A figure illustrating a patch of such turf in a thin place, heavily colonized by the macroscopic foraminiferan *Orbitolites complanata*, is given on Plate XIX, fig. 1.

The fauna and flora of the park vary somewhat from place to place, according to whether the substratum is sandy or rocky, and according to whether it is exposed at low water or lies in a shallow or deeper pool. On the coloured map of Low Isles the depths of the various parts of the park are indicated, and in Text-fig. 8 the relation between the deeper parts (which are sandy in the main) and the more rocky areas is shown. We shall not attempt to describe the rather subtle variations in the series of organisms which present themselves as one passes from rock to sand, from exposed regions to pools, from shallow to deeper water, since this would introduce too many complications. If the illustrations are studied carefully, however, in the light of the paragraphs which follow, a sufficiently clear idea of the variation to be expected should be acquired. The sections of the paper which deal with the rocky area of the flat, the *Thalamita* flat, and the sandy regions, also apply in part to the mangrove park.

The fauna of the mangrove park is not easily characterized. It includes many typical reef flat forms, and shares some species with the mangrove area; it contains a scattered population of living coral, but very much less than the moats; and it has a certain distinction of its own, being the headquarters of some at least of the inhabitants of the reef flat.

Corals recorded from the mangrove park are *Pocillopora bulbosa*, massive *Porites*, *Favia*, *Leptastrea*, *Cyphastrea* and *Heliopora*. They are nowhere abundant, and although there are deep and extensive pools they have no tendency to flourish as in the moats.

Near the mangrove swamp occur some curious areas of bare sand, where the water is rather deep, and there is little or no *Thalassia*, and on one of these a few specimens of the curious jellyfish *Cassiopaea andromeda* were found. This animal lies on its back, unless disturbed, with the fern-like oral arms outspread, so that it looks very like a specimen of the anemone *Actinodendron plumosum*, which is a common inhabitant of sandy places. In an area at Hope Isles comparable to the mangrove park this jellyfish was very common, and there was also a considerable amount of *Heliopora* in the form of platforms.



TEXT-FIG. 8.—To illustrate the distribution of "honeycomb rock" on Low Isles, and the relationship between the deeper pools and the rocky areas in the mangrove park. The conditions are represented only approximately. In the mangrove park the deeper sandy pools alternate in the main with the more rocky areas, suggesting the possibility that the former may be the result of the action of solvents (including mangrove mud during an earlier, more extended phase of the mangrove swamp ?) on a substratum once more uniformly rocky.

The epiphytes and epizoa of the mangrove roots are interesting. Among the former are *Valonia aegagropila*, and a remarkable form of *Turbinaria turbinata*, in which the rhizoidal primitive leaves are profuse and the rest of the frond much reduced. Others are *Caulerpa verticillata*, species of *Ectocarpus*, Cyanophyceae and dendroid colonial diatoms. The epizoa include *Myrionema amboinense*, *Ostrea mordax*, and a large Zoanthid whose polyps (which expand only in the shade) have brown tentacles and a velvet-green disc. A group of these is shown in Plate XXI, fig. 4, half-contracted because of the sunshine. It is a curious fact that although the mangrove roots are in some places so extensively colonized by various organisms, elsewhere they are singularly clean and bare—a state which has been accepted as typical for *R. mucronata*.

The flora may be further characterized. The turf of *Thalassia*, though not universal, is widespread, even on areas which are awash or exposed at low water, and it attains, where thickest, a more luxuriant development than elsewhere on the reef. A notable feature is the abundance of *Halimeda Opuntia* in the turf; this is so marked that the sand in places is largely composed of dead fragments of this alga. *Caulerpa racemosa* and *Halophila ovalis* are other members of the turf, which has very considerable sand-binding properties, due mainly to the rhizomes of the *Thalassia*. A notable alga in the park is *Cystophyllum muricatum*, a species which attains a greater height above the substratum than any other form on the reef. *Caulerpa* may develop long creeping stolons, but *Cystophyllum* attains a height of 4–5 ft.; and with it occur species of *Sargassum*, including *S. lanceolatum*.

Of the animals listed on p. 44, the great majority may be found in the mangrove park; but some are more characteristic of it than others. Beyond the species mentioned, *Melarhaphé* may be found on the trees, and the large black *Pinna vexillum*, the mangrove hermit *Clibanarius striolatus*, and the blue and green crab *Thalamita crenata* are characteristic of the region. Forms which are special features of the park or have their headquarters there are the hydroid *Myrionema amboinense*, the enormous sprawling Holothurian *Synapta maculata* (Plate X, fig. 2), often 2 or 3 ft. long, and the black commercial sponge *Euspongia irregularis* var. *pertusa*. Other species which are very prevalent are the spider-shell *Pterocera crocata*, the round mud-coloured sponge *Cinachyra australiensis*, another sponge, *Spirastrella purpurea*, and the box-crab *Calappa hepatica*. *Holothuria argus*, though nowhere common, is confined to the park and the fringes of the swamp. Of all these animals, the one most distinctly characteristic of the park is *Myrionema amboinense*, a species with large brown polyps which grows on mangrove roots, on *Halimeda*, and on *Thalassia* leaves. This is prevalent where conditions are suitable over an area which includes the mangrove swamp and park, and extends somewhat towards the anchorage. Outside this region it is rarely found.

#### E. THE ROCKY AREA.

(Text-fig. 8.)

Mention has already been made of "honeycomb-rock." This is a descriptive term applied to a type of rock which occurs both on the reef flat and outside the rampart. Since the extent of this rock is important both from the point of view of the origin of the reef and from that of the arrangement of organisms, its distribution should be clearly appreciated, and is illustrated in Text-figs. 7 and 8. The rock in question occurs in the form

either of flattened slabs, often of considerable extent, or of more or less continuous pavement-like areas. The surface is irregular and the rock is honeycombed by pits and intricate crevices, and is attacked by boring organisms. The rock consists of dead coral, but probably in a modified form.\*

Outside the rampart the honeycomb-rock is present along two stretches. The "windward shelf" of the key chart, a crescentic pavement fringing the windward arc of the reef, is composed of it; and the "south-west shelf" is a smaller area of similar nature. We do not wish to imply that honeycomb-rock inside and outside the rampart is of the same chemical composition and origin, though this may be the case. On the flat itself, inside the rampart, the rock occurs most extensively over a broad curved tract indicated by close stippling in Text-fig. 8. This tract starts at the rampart and runs at first northward and slightly westward, afterwards tending north-eastward in the direction of Tripneustes Spit; but becomes lost in the sandy part of the anchorage before the Spit is reached. This area is not wholly rocky, since it contains sandy pools and shingle-patches; nor is the rock equally developed all over it; but it is the region in which the rock is of maximal occurrence. As indicated in the figure by less close stippling, rocky areas occur also in the mangrove park east of the principal tract, and extend into some of the moat pools and on to the Thalamita flat. The contrast between these patches and the main tract is probably exaggerated in the figure; but the rock is on the whole more broken in the mangrove park than it is in the principal tract. It is this rocky tract, together with the rampart, which holds up the water in the south-eastern part of the mangrove park during the period of low water.

The rocky tract lies partly within the mangrove park, since part of it is colonized by trees or saplings of *Rhizophora*. The park, however, extends farther than the rocky tract, on to sandy ground, in the region between the anchorage and the mangrove swamp. The inhabitants of the rocky part of the park will resemble those of the rocky tract or those of the Thalamita flat according to the exact nature of the ground.

The fauna and flora of the rocky tract are not markedly distinct from that of any part of the reef flat where dead blocks of coral are present, but on it rock-haunting species are naturally somewhat concentrated. A striking feature in some places is the abundance of *Onchidium*. This soft and leathery pulmonate, similar in facies to a Dorid nudibranch, is seen by the score, out of water and exposed to the full power of the sun. On a single square yard fifteen individuals were counted. Other common inhabitants of the region are the mud-coloured, very hairy crab, *Pilumnus vespertilio*; the black or variegated brittle-star, *Ophiocoma scolopendrina*; *Cinachyra australiensis*; *Acanthozostera gemmata*; and *Holothuria atra*, with its tail anchored beneath a block of coral or in a crevice. Attached lamellibranchs are naturally abundant (*Modiolus auriculatus*, *Spondylus ducalis*, *Chama jukesii*) and the rock is attacked by boring species. A low moss-like turf of algae often clothes the rock; this is variable in constitution from one place to another, but frequently includes *Laurencia*; *Boodlea* and *Dictyosphaeria* are also characteristic.

The shingle-banks F9 and F10 may conveniently be mentioned here. They are areas consisting of rampart material, and their fauna and flora resemble those of the rampart, grading imperceptibly, in the case of F9, into those of the Thalamita flat. A notable inhabitant of F9 is the calling-crab *Gelasimus tetragonon*.

\* Sections and analyses will be published later.

## F. THE THALAMITA FLAT.

This is a wide stretch of reef flat consisting in the main of sandy ground overlaid by slabs and boulders of dead coral, but also includes honeycomb rock. It is partly exposed at low water, partly under very shallow pools; but only exceptionally are the pools deep enough to contain a population resembling that of the moats. The sandy areas support *Thalassia* and *Halophila* as usual, and also *Spyridia filamentosa*. Except in the moat-like pools mentioned, and in the regions of transition from flat to moat, there is little living coral, such as exists being limited to shallow fringes of living *Porites* round the edges of dead slabs, and to small examples of *Favia*, *Cyphastrea*, etc.

The Thalamita flat is a region in which organisms characteristic of the undersides of movable slabs and boulders are particularly concentrated, though under similar boulders elsewhere a comparable range of life will be found. On the upper surfaces there are *Chama*, *Spondylus*, acorn-barnacles and limpets (*Siphonaria*), but the species of the undersides are more interesting. A striking feature here are the encrusting sponges, of which a number of species are common, and exhibit diverse and brilliant coloration. The list which follows will give some idea of the range both of species and colour. The algae of the region consist mainly of mossy growths in which *Laurencia*, *Boodlea* (and in the spring, *Hydroclathrus*) are dominant. *Dictyosphaeria* is widespread, and the underside forms include *Anadyomene*, nullipores and Squamariaceæ.

Another characteristic of the Thalamita flat is the abundance of *Hippopus hippopus* (Plate XVIII, fig. 1), adults of a similar range of size being evenly distributed. Young specimens are scarce.

## LIST ILLUSTRATING THE FAUNA OF THE THALAMITA FLAT.

## PORIFERA.

- Gellius fibulatus and the following encrusting forms:  
 Chondrilla nucula.  
 (Buff; greyish or pinkish lavender; liver-colour.)  
 Chalina clathrata.  
 (Black.)  
 Chalina camerata.  
 (Cream.)  
 Desmacidon reptans.  
 (Lilac-blue.)  
 Ophlitaspongia rimosa.  
 (Usually red or scarlet.)  
 Rhaphidophlus coralliophilus.  
 (Red.)  
 Iotrochota purpurea.  
 (Indigo-blue; dark blue; black.)  
 Laxosuberites proteus.  
 (Golden yellow.)  
 Pseudosuberites andrewsi.  
 (Brown.)

## PORIFERA—continued.

- Polymastia sp.  
 (Yellow.)  
 Spirastrella semilunaris.  
 (Probably includes scarlet, yellowish or reddish brown, and brilliant ultramarine forms.)  
 Spirastrella aurivillii.  
 (Flesh-colour.)

## COELENTERATA.

- Phymanthus.  
 Stoichactis kenti.  
 Actinodendron plumosum.  
 Dynamena crisioides.

## POLYCHAETA.

- Iphione muricata.

## BRACHYURA.

- Thalamita stimpsonii.  
 Atergatis ocyroe.  
 Pilumnus vespertilio.

## GASTROPODA.

Trochus fenestratus.  
Siphonaria denticulata.

## LAMELLIBRANCHIA.

Spondylus ducalis.  
Lima tenera.  
Pinctada margaritifera.  
Arca fusca.  
Hippopus hippopus.  
Chama jukesii.

## ECHINODERMATA.

Ophiothrix longipeda.  
Stichopus horrens.  
Holothuria atra.  
„ coluber.  
„ impatiens.  
„ leucospilota.

## ASCIDIACEA.

Didemnum candidum.  
„ psammatodes var. skeati.

## G. THE SANDY AREAS.

(Plate VIII, fig. 1.)

The Thalamita flat passes gradually along its northern side into the Sand flat. The latter is the most extensive sandy part of the reef flat, and has definite sandbanks (F2-4) between it and the anchorage. The region between anchorage and mangrove park, however, is also extensively sandy, and includes the sandbanks F6, 7 and 8. The region between F7 and 8 and the mangrove swamp, which lies partly within the limits of the mangrove park, is also so sandy that it may be considered with the others.

Some of the sandy areas are bare and free from plants, but usually there is at least a sparse growth of *Thalassia*, *Halophila*, or both; but whereas *Halophila* is sometimes dense, *Thalassia* is usually sparse, and often covered by epiphytes (*Spyridia filamentosa*, *Polysiphonia*, etc.). On the Sand flat, which is partly exposed at low water, partly covered by very shallow pools, *Thalassia* tends to keep to the pools, whereas *Halophila*, *Spyridia* and beard-like growths of Cyanophyceae occur freely both in pools and on the exposed parts. In April, 1929, these Cyanophyceae became notably abundant on various parts of the reef flat and in the anchorage, overgrowing and tending to smother living coral in the latter locality. On the Sand flat and Thalamita flat they were particularly prevalent on the eastern side. The form characteristic of the shallower areas is *Lyngbya majuscula*, but mixed with it is usually *Hormothamnium solutum*, which replaces it in the deeper pools. On Plate VIII, fig. 1, the desolate aspect of the Sand flat with its trailing beards of Cyanophyceae may be seen. A striking alga confined to sandy areas is *Avrainvillea erecta*, which was first noticed on 24th October 1928, and thereafter was abundant. The carrot-like stipes of this species, 6 or 8 in. long, is immersed in the sand, only the crown, which resembles a green sponge, projecting at the surface. *Caulerpa racemosa*, though present, plays no extensive part in sand-binding here. Both here and on the Thalamita flat *Sargassum* and *Cystophyllum* appear in pools.

The fauna of the sand is interesting and distinctive. The anemone *Actinodendron plumosum* is a characteristic form, burying its trumpet-shaped body in the sand and expanding its fern-like fronds (Plate XX, fig. 1) at the surface when covered by water. When exposed it partially contracts into its burrow, or lies with its upper parts collapsed at the surface. Most of the animals, however, live out of sight, either in burrows or buried in the sand. On p. 56 is a list of common or interesting species.

This list requires further comment. In the first place, it might be expected that among the worms some species of polychaet would be dominant. As far as we could ascertain by a good deal of digging this is not the case. The commonest "worm" is one

of the species of *Edwardsia*, which comes up in almost every spadeful of sand. After this, the very large *Balanoglossus carnosus* (the castings of which are visible on the surface, making an estimate of the population possible) is among the prevalent species; and other plentiful forms are gephyreans, such as *Aspidosiphon cumingii*, which resembles a piece of *Thalassia* root; the polychaet *Mesochaetopterus minuta* with its long thin tubes; and the attenuated *Phyllodoce malmgreni*. *Eurythoe complanata*, a handsome polychaet, is common on the reef, but occurs under boulders, etc., as well as in sand. Among the mollusca various forms are common. Naticidae of a number of species occur, more than those mentioned in the list. *Nassarius coronatus* is very common, and may be seen exploring the surface with a long feeler, either in pools or when the flat is covered by the tide. *Strombus gibberulus* is a leaping buried form; *S. luhuanus* sometimes occurs in large colonies, lying about the surface. *Terebra affinis* and *Clava vertagus* are the usual reward of anyone digging for the handsome pencil-shell *Terebra muscaria*. One of the most interesting forms is the giant squilla *Lysiosquilla maculata*, which makes a very deep burrow, some 3 in. in diameter, narrowed at the mouth by a circular shelf or diaphragm. *Ptychodera flava* (a small Enteropneust), and a sand-dwelling species of the Actinian genus *Phymanthus*, are locally abundant. The Cerianthid *Arachnanthus* was rarely seen.

If a complete list of the inhabitants of the sandy areas were to be made, it would contain not only typical sand-dwellers, such as those mentioned and many beside, but would also include a very considerable number of the species given in the list of typical reef-flat organisms on p. 44. This is due, however, simply to the fact that a certain number of scattered pieces of dead coral and specimens of *Hippopus* occur on predominantly sandy areas, and upon or beneath these the species in question are found.

#### SPECIES CHARACTERISTIC OF SANDY AREAS.

##### ANTHOZOA.

*Arachnanthus*.  
*Edwardsia*, two species at least.  
*Phymanthus*.  
*Actinodendron plumosum*.

##### NEMERTINEA.

*Baseodiscus* (probably *B. quinquelineatus*).  
 Species of *Lineus*.

##### POLYCHAETA.

*Eurythoe complanata*.  
*Phyllodoce malmgreni*.  
*Marphysa mossambica*.  
*Scolelepis indica*.  
*Mesochaetopterus minuta*.

##### GEPHYREA.

*Aspidosiphon cumingii*.

##### CRUSTACEA DECAPODA.

*Callianassa australiensis*.  
*Callianidea*.  
*Macrophthalmus telescopicus*.

##### STOMATOPODA.

*Lysiosquilla maculata*.

##### GASTROPODA.

*Clava vertagus*.  
*Natica gualteriana*.  
*Uber flemingianum*.  
 „ *mammilla*.  
*Strombus gibberulus*.  
*Nassarius coronatus*.  
*Terebra affinis*.  
 „ *muscaria*.

##### LAMELIBRANCHIA.

*Loripes edentulus*.  
*Corbis fimbriata*.  
*Cardium oxygonum*.  
*Tellina virgata*.  
*Mactra maculata*.

##### ECHINODERMATA.

*Archaster typicus*.  
*Laganum depressum*.  
*Holothuria arenicola*.

##### ENTEROPNEUSTA.

*Balanoglossus carnosus*.  
*Ptychodera flava*.



## THE RAMPARTS AND BOULDER TRACT.

## A. THE OUTER RAMPART.

(Text-figs. 7 and 12 : Plate XI ; Plate XII, figs. 1 and 2 ; Plate XIII, fig. 1 ; Plate XXVII.)

The extent of the outer rampart may be appreciated at a glance from Text-fig. 12, where it is shown in solid black. With it have been included Tripneustes spit and Asterina spit, which, although they hardly belong to the rampart proper, may suitably be considered with it, since they resemble it both structurally and ecologically.

ENCROACHMENT OF THE RAMPART.—The inner edge of the rampart is abrupt, forming in most places a slight cliff or escarpment. Its neatness, and steep slope, suggest that it is being renewed by fresh additions of shingle, and is tending continually to encroach upon the flat or upon the inner rampart. That such encroachment does indeed take place is illustrated by four of our photographs. Plate XI, fig. 4, is a view from above, looking down upon a portion of the Madrepora moat. In the upper part of the figure living coral may be seen ; in the lower part, shingle from the rampart which has fallen upon the coral. Plate XII, fig. 1, is a view including part of the outer rampart and part of the inner. The steep slope of the outer rampart is seen on the right, and at its foot a bush of *Avicennia officinalis*. The outer rampart just here encroached decidedly upon this bush during our year of residence. This figure also shows a secondary wave of clean shingle which is overrunning the main mass of the outer rampart. Such secondary waves are indicated on the key chart by dotted lines running across the bases of some of the inward promontories of the rampart (R3, R6, R7), and may be seen in the aerial photographs reproduced in Plate XXVII. Where this happens organisms characteristic of the inner rampart (isopods, ants, and *Avicennia*) tend to appear on the piece of outer rampart cut off by the new shingle wave. Plate XIII, fig. 1, illustrates a case in which long spits of outer-rampart shingle have overrun the inner rampart.

Where the escarpments of either the outer or the inner ramparts descend to a moat or pool, the interstices of the shingle may harbour an interesting fauna. In the case of the pond P9 and neighbouring regions, for instance, there is a large population of the small actinian *Anemonia citrina*, as many as 40 specimens being found on one fragment of shingle.

THE RAMPART AS A HABITAT.—The outer rampart offers at first sight a most unpromising field for colonization by plants or animals. It resembles an ordinary pebble-beach, but, instead of pebbles, consists of loose fragments of dead coral and shells (Plate XI, fig. 3). This debris includes the remains of a variety of corals, but species belonging to the genus *Acropora* predominate. Although as a habitat the rampart is, therefore, in a certain degree unstable, its stability (except, presumably, in abnormally heavy weather) is greater than appears, since the angular and nodulated nature of the shingle fragments results in a good deal of interlocking, in addition to which they function as breakwaters. There is very little tendency towards any cementing of the fragments, at least near the surface ; and although nullipores in the form of thin crusts are a feature of the rampart, they have here no binding power and make no continuous sheets of growth such as characterize the Outer Barrier. In spite, however, of the limitations of the rampart as an environment for life, it conceals an enormously populous fauna, particularly of small crabs and gastropods, under the fragments. Very little surface life is visible.

VARIATION IN LEVEL AND CORRELATED ZONATION.—The key to the distribution of life on the rampart is provided by a map, for which we are indebted to M. D. Glynn, and which illustrates the distribution of the encrusting nullipores upon it. These are arranged in a series of band-like zones running parallel to the general course of the rampart. The map will be reproduced and fully described in Tandy's systematic report on the algæ; but the essential point which it illustrates is that the zonation of nullipores conforms to the following plan:

1. In the highest and driest parts nullipores are absent or nearly so.
2. In a zone slightly nearer the sea they are slightly developed *under* fragments.
3. In the next zone to seaward they are moderately developed and visible *on the surface*.
4. In the last zone nullipores are *plentiful* on the surface, so that the ground is visibly purplish with them.

The zonation of other forms of life follows this plan, and it depends principally upon level. The rampart reaches higher levels along the stretch between the mangroves and the sea than it does to westward. From near the point M6 it slopes gradually downward in a westerly direction to the gap B, becoming slightly higher again on the stretch RA, but nowhere as high as to eastward. This means that in its western part the highest zone, in which nullipores do not exist, is absent. Other effects of level are due to the facts that the highest parts are the longest exposed during the period of low water; and that in many places the lower parts are kept moist during the ebb by water trickling off the flat, which, it will be remembered, is on a higher level than the sea outside the rampart at low water of a spring tide. Regions in which this trickling is well marked are indicated on the key chart as "trickle-zone." In certain places in this zone there is, contrary to the general rule, a binding of the shingle by turfs of algæ (Plate XIX, figs. 2 and 4), the most remarkable of which is a form of *Caulerpa racemosa*. Some idea of the zonation of the rampart may be formed from Plate XXVII.

In the highest and driest parts of the rampart little life is to be found beyond rapidly moving isopods. With the exception of these regions, the rampart shelters a number of creatures, mostly under the shingle, some of which are very abundant—small gastropods (especially species of *Nerita*) and crabs (including many rapid scuttlers) predominate, but there are also echinoderms (*Asterina exigua*, *Echinometra mathaei*, and small holothurians), small hermits, lamellibranchs and anemones. Some of these forms, especially the mollusca, probably exhibit fairly precise zonation according to level, but we were unable to make any detailed study of it.

GAPS IN THE RAMPART.—The gaps which occur in the rampart, and which are marked A, B, C and D on the key chart, are not actual interruptions in its course, but merely low places through which the tide flows before the rampart in general is submerged. Their fauna and flora is slightly modified as a result of these conditions.

THE BOULDER ZONE OF THE RAMPART.—Along its seaward margin the rampart merges either into the windward shelf or into a zone in which boulders are conspicuous ("boulder zone" of the key chart). Here the fauna and flora become more varied, but it is impossible to draw any hard and fast line ecologically between the seaward edge of the rampart and the shoreward parts of these other regions. The boulder zone has a rather characteristic population, the nature of which may be judged from the following list, in which a number of its common animals are marked with asterisks. The algæ are

enumerated farther on, on p. 68. The population of individual boulders depends, of course, partly upon the level at which they occur.

ORGANISMS CHARACTERISTIC OF THE OUTER RAMPART AND BOULDER TRACT.—The following list covers the boulder *tract* as well as the rampart and its boulder *zone*. The species cannot be listed separately for these areas, since the series characteristic of each run into one another, and sufficient indication has already been given of the manner in which the various forms are arranged. The list illustrates the predominance of mollusca and crustacea over other groups of animals; it includes a number of forms capable of withstanding arid conditions of one sort or another during the period of low water; and forms which can make the best of the unpromising environment presented by a shingle bank. Shells of the cat's-eye (*Turbo petholatus*) are common on the rampart, but we have not taken the living animal, even when diving.

#### ANIMALS CHARACTERISTIC OF OUTER RAMPART AND BOULDER TRACT.

(A number of species common in the boulder zone of the rampart are marked with asterisks.)

##### COELENTERATA.

- Small anemones of the Anthopleura and Phellia types.
- Dynamena crisioides.

##### SIPUNCULOIDEA.

- \*Aspidosiphon.
- \*Cloeosiphon.
- \*Physcosoma.

##### CIRRIPIEDIA.

- Acorn-barnacles.

##### ISOPODA.

- Ligia australiensis.

##### AMPHIPODA.

- Locally abundant; including a species of Hyale.

##### ANOMURA.

- Clibanarius virescens.
- Petrolisthes lamarecki.

##### BRACHYURA.

- Thalamita admete.
- Chlorodopsis melanochirus.
- Actaea tomentosa.
- Atergatis ocyroe.
- Phymodius unguatus.
- Leptodius exaratus.
- „ nudipes.
- Metopograpsus messor.

##### STOMATOPODA.

- Gonodactylus chiragra.

##### AMPHINEURA.

- \*Acanthozostera gemmata.
- Schizochiton incisus.

##### GASTROPODA.

- \*Trochus niloticus.
- Turbo nivosus.
- „ porphyrites.
- Nerita albicilla.

##### GASTROPODA—continued.

- Nerita chamaeleon.
- „ plicata.
- „ polita.
- „ striata.
- Planaxis sulcatus.
- \*Cypraea annulus.
- „ erroneus.
- Drupa marginalba.
- „ tuberculata.
- \*Siphonaria denticulata.
- \*Onchidium.

##### LAMELLIBRANCHIA.

- \*Ostrea mordax.
- Melina nucleus.
- Modiolus auriculatus.
- \*Lithophaga argentea.
- \* „ cumingiana.
- \* „ obesa.
- \* „ subula. = *hanleyana* in Otte, 1957
- \* „ teres.

- Arca fusca.

- \* „ imbricata.
- \*Tridacna crocea.

- \*Gastrochaena gigantea. = *cuneiformis* in Otte, 1957

##### ECHINODERMATA.

- Asterina exigua.
- Echinometra mathaei.
- Ophiocoma scolopendrina.
- Small or young Holothurians, including
- Polycheira rufescens.
- Holothuria erinaceus.
- „ leucospilota.
- „ pardalis.

##### ASCIDIACEA.

- \*Didemnum candidum.

## B. THE BOULDER TRACT.

(Plate V, figs. 3 and 4.)

This region calls for little in the way of special comment. It is the tract along which the boulders of dead coral attain a larger average size than elsewhere, and it contains also a proportion of smaller coral fragments and some shingle. Its flora and fauna are, therefore, a reflection of those of the rampart and boulder zone already described. A feature of special interest is the notable boulder covered with *Ostrea mordax* and illustrated in Plate V, fig. 4, which has already been described (p. 36). The tract is a region particularly favourable for the study of the boring lamellibranchs and gephyreans which are a general feature of coral rock and boulders on the reef. These are described fully in a report by G. W. Otter elsewhere in this series, but it may be mentioned here that they include several species of the genera *Lithophaga* and *Gastrochaena*, as well as other forms, such as *Modiolus cinnamomeus*, *Petricola lapicida*, etc. *Tridacna crocea* is one of the most notable borers, since it is present in incredible numbers and is responsible for the excavation of cavities of considerable size. This species is illustrated in Plate VI, figs. 3 and 4, in different degrees of submergence in the surrounding coral. It is often buried so fully that the expanded mantle is flush with the surface. The gephyreans include a number of Sipunculid forms belonging to the genera *Aspidosiphon*, *Cloeosiphon*, *Physcosoma*, etc., notable among them being a species of *Aspidosiphon*, a stout worm with a conical striated extremity more than a centimetre in diameter.

Some of these animals are of relatively large size, and make very considerable burrows in the coral; the total population of them is enormous, and considered as a unit in reef economy they represent a very powerful destructive agency.

## C. THE INNER RAMPART.

(Text-figs. 7 and 15; Plate XII, figs. 1, 3 and 4; Plate XIII, figs. 1-3; Plate XXVII.)

This region differs from the outer rampart rather sharply in an ecological sense.

In the first place the area is extensively colonized by certain flowering plants, which show some relation to tide levels. Immediately inside the outer rampart young seedlings and saplings of *Rhizophora mucronata* may be seen (Plate XI, fig. 2), and near the edge of the mangrove swamp are a number of outlying specimens of it, in a dead or dying condition (Plate XIII, fig. 3). Bushes of *Avicennia officinalis* (Plate XII, fig. 3), often distorted in shape, are scattered over the inner rampart, and another interesting plant is *Aegialitis annulata*. On the higher parts the shingle is extensively covered by the creeping *Sesuvium Portulacastrum* (Plate XIX, fig. 3). Indeed, at the end of the shingle tongue R2 there is a field of it some 100 yds. long by 30 wide (Plate XII, fig. 4, and Plate XXVII). The isolated patches of inner rampart at either end of the main area (IR1, 2, 3 and 17) have a fairly dense population of *Avicennia*, together with vestigial representatives of *Rhizophora* and some *Aegialitis*. It is a curious fact that on this reef the main population of *Avicennia* lies between the mangrove swamp (*i. e.* the home of the main population of *Rhizophora*) and the sea. This, in a coastal area of even slope, would be the other way round; but at Low Isles the inner rampart is *higher* in level than the floor of the *Rhizophora*-swamp, hence the inversion.

The fauna of the inner rampart exhibits a mingling of outer rampart species with forms characteristic of the shingle tongues inside the mangrove area, and includes the species listed below. Small gastropods and crabs are the dominant forms. The fauna of the moat-like pools which occupy the angle between the inner and outer ramparts has already been described; and it is only necessary to add that in regions bordering on such pools, and in other places where the surface is damper than usual, the fauna becomes somewhat modified, and richer in species. With regard to the calling-crab of the inner rampart, *Gelasimus tetragonon*, which sometimes makes its burrows in extraordinarily hard material, this species is known to occur at Low Isles only in areas outside the mangrove swamp. It inhabits the shingle-bank F9 as well as several parts of the inner rampart.

## SPECIES CHARACTERISTIC OF INNER RAMPART.

## ISOPODA.

*Ligia australiensis*.

## ANOMURA.

*Clibanarius virescens*.

*Petrolisthes lamarcki*.

## BRACHYURA.

*Scylla serrata*.

*Leptodius exaratus*.

*Sesarma bidens*.

„ *villosa*.

*Metopograpsus messor*.

*Gelasimus tetragonon*.

## INSECTA.

Ants.

## AMPHINEURA.

*Acanthozostera gemmata*.

## GASTROPODA.

*Turbo porphyrites*.

*Nerita albicilla*.

„ *plicata*.

„ *striata*.

*Bembicium melanostoma*.

*Tectarius malaccanus*.

*Melarhaphe scabra*.

„ *undulata*.

*Planaxis sulcatus*.

*Quoyia decollata*.

## THE ANCHORAGE.\*

(Plate V, fig. 1; Plate XIV.)

In describing the reef flat enough has been said to cover the shallower regions bordering the anchorage. It remains therefore only to consider the reefs of dead coral rock, overgrown by living coral, which fringe it. These are labelled A1-5 on the key chart.

In the anchorage and the other seaward slopes of the reef, we are dealing for the first time with zones in which a varied growth of living coral and alcyonaria in a flourishing condition is the primary characteristic. In the moats, it is true, coral growth of a peculiar description is abundant, but it is restricted to a small number of species; and although in a pool such as the western moat a considerable number of coral species are represented, they cannot, apart from the special moat species, be described as constituting a flourishing growth. In the anchorage and on the seaward slope, however, wherever there is sufficient depth of water, and so long as no special local conditions of a limiting nature prevail, corals abound both in species and individuals, and form rich and varied fields of growth. Some idea of the extent and variety of such living coral may be gained from Plate XV,

\* The anchorage, although its floor forms part of the general seaward slope of the reef, is an inlet in which special conditions prevail, and is therefore treated separately here.

which shows, in a diagrammatic form, the corals in an area some 6 ft. wide and 8 ft. long in the anchorage. It will be observed that almost the whole field here is occupied by living and overlapping colonies, so that the area of bare rock exposed is very slight.

The reefs of the anchorage consist of very irregular masses of dead coral, with sand, or sand and debris, between them. As the floor of the anchorage slopes downwards away from the shore, the height of such of these masses as reach the level of low water naturally increases. Near the shore, therefore, the pools or channels between them are shallow, becoming deep further out. The seaward margins of the reefs are usually somewhat abrupt.

The greater part of the area of these reefs is accessible only at low spring tides. The degree of their exposure may be illustrated by an example. Luana reef, across which a level traverse was taken, is divided rather distinctly into a slightly higher landward part (A1) and a lower seaward portion (A2). The landward region uncovers at any tide which falls to a level 0·8 ft. above datum. The seaward part is submerged at such a tide, but at the lowest springs (the extreme recorded being 0·4 ft. below datum) its highest parts are exposed; its deeper regions are therefore always submerged.

AREAS OF HIGH LEVEL.—The region A1 just mentioned is of particular interest. As a result of its level it is exposed or awash more frequently and for longer periods than the rest of Luana reef, though submerged at neaps. This difference, though slight, is enough to modify its coral fauna distinctly. A considerable part of the area is occupied by a platform-like growth of *Montipora ramosa*, with *Acropora hebes* and other corals, somewhat similar to the growth in the moats. Beside these are various other corals and alcyonaria, numerous clams, holothurians and other animals, and a considerable growth of certain algae. The most interesting feature, however, is the presence of a quantity of a species of *Acropora* with slender buff-coloured branches and pale blue tips. This species (*A. pulchra*) makes large rounded bushes or tufts (Plate IX, fig. 2), or even platforms, which are exposed at low spring tides, and which occur chiefly on the more seaward part of the area. This coral appears to be characteristic of a somewhat precisely limited zone of the shore, occurring normally neither above nor below the region peculiar to it. It may be found, however, in any suitable position on the Low Isles reef which is directly open to deep water and which lies at the level required (just above datum).

On other anchorage reefs there occur certain areas of similar level to A1—for instance, the middle of the island-like reef A3—but they are less interesting. In Plate XIV, fig. 1, a view from the top of the lighthouse shows most of the area A1 and also the higher parts of A3, with a deep channel between. This photograph was taken at a state of the tide which left A1 exposed and the more seaward part of the same reef (A2) still under water. This brings out well the difference in level between A1 and A2, the latter area being dimly visible beneath the water.

AREAS OF LOWER LEVEL.—On the seaward part of Luana reef and in comparable regions the coral growth at once becomes denser and more varied, although naturally richer in some places than in others. Plate XV represents a portion of A2 close to the channel which separates it from A3. Plate XIV, fig. 2, illustrates the growth at a point nearer the shore.

The coral fauna of these reefs is characterized by the abundance of species belonging to the genus *Acropora*, but presenting widely varied aspects. Some of them form large salver-shaped or bracket-like structures with a stout central or eccentric stalk or region of attachment; others form bushes or straggling areas of stag's-horn-like branches; still



TEXT-FIG. 9.—Sections of the seaward slopes of the Low Isles Reef. Their positions on the reef are indicated in Text-fig. 11, each section bearing the same number here as in Text-fig. 11. The slopes are described on p. 64.

others make finely divided bushy growths of completely different facies. Another dominant series are the foliose species of *Montipora* also illustrated in Plate XV. Beyond these a variety of other forms are represented. We do not propose to describe the growth-forms and ecological relationships of the coral fauna here, because, in considering the ecology of the reef as a whole, we feel that our account will be the more intelligible if digressions dealing with corals in particular are avoided. Discussions of the ecology of corals will be found, however, in papers farther on in this volume.

The alcyonaria, no less than the corals, find their proper habitat in the anchorage and on the seaward slope. They are not wholly absent from the flat, but are of occasional occurrence there, and do not attain a large size; they possess no representatives which flourish actively under moat conditions. In the regions to which open water has access at all states of the tide, they become represented in hardly lesser degree than the corals, exhibiting great abundance of species and occupying a large amount of space as individuals. Specimens of *Sarcophytum* from 2-4 ft. across are not rare (Plate XVI, fig. 1), and fields of *Simularia* covering yards of rock also occur (Plate XVI, fig. 2). Specimens of some of the large fleshy species may occur at levels where they are liable to exposure at low water (Plate XVI, fig. 3). These lie flaccid until the water returns, when they become turgid once more and appear to be none the worse.

FAUNA AND FLORA OF THE ANCHORAGE.—The nature of the fauna and flora of the anchorage may be gathered from the list on p. 67. This list includes the rest of the seaward slope as well as the anchorage, but the majority of the forms mentioned are common to both. In the anchorage the variety of animals other than corals and alcyonaria is considerable, despite the prevalence of forms belonging to these groups. Clams in particular are abundant, and algae are well represented on the higher levels. As levels below low water of springs are reached, however, algal growth becomes very poor, and corals, clams and alcyonaria appear to be completely dominant. In April 1929, the coral became much infested by a beard-like alga similar to *Lyngbya majuscula*.

## THE SEAWARD SLOPES OF THE REEF.

(Text-figs. 9-11; Plate XVII, fig. 1.)

THE CONFIGURATION OF THE SLOPES.—From the outer rampart and the boulder tract, the reef descends to the muddy floor which surrounds it. The slopes are everywhere rocky except in the anchorage. We owe our knowledge of the configuration of these slopes to soundings taken by M. A. Spender, with the assistance of Anne Stephenson. Some of the lines of soundings have been tabulated in the form of sections, and are reproduced in Text-fig. 9. The positions of these several sections on the reef are indicated in Text-fig. 11 (p. 68).

It will be evident from section 3 in Text-fig. 9 that at the windward arc of the reef the seaward slope is at first gradual; but when a depth of 21 ft. (6.4 metres) is reached, it suddenly becomes steep, descending to 48 ft. (14.6 m.) in the next 13 yards. The slope here, therefore, reaches the inclination of 1 ft. in 1.4. From the bottom of this descent the slope becomes more gradual again, until it reaches 86 ft. (26.2 m.) at a distance of 360 yards from E beacon. From that depth to seaward the level rises again slightly, to 70.5 ft. (21.5 m.); in other words, there is a slight trough at the foot of the slope.



Neither of the sections 2 and 4 reveals anything as remarkable as this; but both indicate the same tendency towards a gradual slope from the shore-line, followed first by a steeper slope and then by a more gradual one. The steeper part begins at comparable distances (about 170–190 yards) from the shore\* but the slope varies from 1 in 4·2 to 1 in 6·2, and does not approach the inclination which occurs at the windward arc. The maximum depths reached along these sections vary from 55 ft. (16·8 m.) to 76 ft. (23·2 m.) at distances of some 300 yards from the shore. The steeper of the two slopes and the one descending to the greatest depth (apart, of course, from the windward slope first described) lies off the extreme western corner of the reef (section 4).

Other lines of soundings not illustrated here provide further data. The most important of them was taken to leeward of the boulder tract (5, in Text-fig. 11). Here the slope is in the main quite gradual, the maximum depth reached being 37 ft. (11·3 m.) at 294 yards from the boulder tract. There is, in fact, a shoal to leeward of the reef, which deepens gradually and merges into the 11- to 12-fathom level some three miles to the north-west. Numerous soundings off the mouth of the anchorage give depths of 21 to 29 ft. (6·4 to 8·8 m.).

#### THE FAUNA AND FLORA OF THE SLOPES.

THE FRINGE TO SEAWARD OF THE RAMPART.—The zone of boulders into which the rampart merges along much of its extent has already been mentioned (p. 58), but a further note is required regarding the “windward shelf” and “south-west shelf” of the key chart.

The windward shelf is a pavement of pitted honeycomb-rock, considerably overgrown by a felt of algae. There are boulders and debris on its surface. The algal flora of the honeycomb-rock and boulder zone includes the forms listed on p. 68, but among these the brown alga *Sargassum cristaeifolium* is particularly noteworthy. This species is a form of higher growth than most of the others, and is more or less abundant all along the windward shelf, where it constitutes a distinct “*Sargassum* zone,” in which *Turbinaria ornata* is also a characteristic element. The algal zone in general is widest and most luxuriant at the weather extremity of the reef, and the growth of *Sargassum* at its best where the trickle from the rampart is well marked. The strip of *S. cristaeifolium* and *T. ornata* is also represented outside the stretch of rampart RA. The well-known *Chlorodesmis comosa*, forming tufts of the most brilliant green, is found both on the windward shelf and on the south-west shelf. It is a form characteristic of the Outer Barrier and of the outer slopes of Batt Reef, but does not occur on the flat at Low Isles. An interesting animal to be found both in the boulder zone and off shore is a species of the Zoanthid genus *Palythoa*, large masses of which may be completely exposed at low water (Plate VI, fig. 3.).

THE PRINCIPAL SLOPE (Text-figs. 9 and 10; Plate XVII, fig. 1).—From the windward shelf or the boulder zone the transition to the region of effective coral growth is usually gradual, though more rapid in some places than in others. At first small, low or isolated colonies of corals and alcyonaria appear, but as the water deepens these rapidly increase in size and number until a rich growth is attained. The seaward slope, however, is not covered uniformly by a carpet of coral. The surface of the slope, to begin with, is not smooth, nor merely slightly irregular; it is in most places definitely rugged, being covered by fixed blocks of dead coral of varying shape. These blocks are low and broad near the

\* *I. e.* from B and D beacons respectively.

shore, but as the depth of the water increases, they tend to become higher, and many of them form very large mounds. From the shore outwards for some distance, the tops of a number of these mounds are at such a level that they are exposed at low water of exceptional tides. These masses may be as much as 20 by 25 ft. across the top, with sides 20 ft. or more deep, which are frequently precipitous or overhanging, so much so that in the extreme cases the mass becomes more or less mushroom-shaped. It is the tendency of coral to grow on top of these masses of rock, and down their sides. Overhanging surfaces present a sparser growth, and many of the species characteristic of them are forms which rarely if ever appear in the more sunlit positions. The floor of the slopes between the rocky masses is usually either bare or but poorly colonized.

Much of what has just been described lies beyond the level of low water of the most extreme tide, between that and a depth of some 5 fathoms. The description of this submerged region is based upon examinations of the slope made with the assistance of a diving helmet, supplemented by a study with a water telescope used from a boat.

The belt of rich coral growth encircles the whole reef. At the same time it is more luxuriantly developed in some places than in others, and differences exist in the range



TEXT-FIG. 10.—Section of a slope to leeward of Low Isles, illustrating the arrangement of coral masses upon it. For comparison with Plate. XVII, fig. 1; see also p. 65. This section is not based upon data as precise as those reproduced in Text-fig. 9, but is founded upon information sufficiently definite to give it an approximate accuracy. The vertical and horizontal scales are the same.

of species and growth-forms represented, as well as in other respects, between the windward and leeward sides. The “coral heads”\* or mounds of rock overgrown by living coral, reach their most exaggerated form on the leeward side. A distinct zonation of coral species on the slopes is recognizable. The subject of this paragraph will be considered more fully in subsequent papers.

Before closing our account of the seaward slope and anchorage, we must mention an important but elusive section of the fauna. Wherever and whenever one dives in these regions, the water is seen to be populated by innumerable fishes. The brilliant and varied species characteristic of coral reefs abound, and the total population must be enormous. Many of the smaller fish are commensal with coral, as many as forty or fifty sheltering among the branches of a single colony of moderate size. We have seen some of these fish eating living alcyonaria, and others nibbling microphytic algae from the rock. We have not seen living coral attacked, but if part of a colony dies that portion may be devoured at once.

\* We have not used the terms “niggerhead” or “negrohead” in this report, because they seem to involve ambiguity. We refer to stranded blocks of dead coral as “boulders,” and to masses of dead coral covered by a living growth as “coral heads,” this latter being the usage of the pilot-books.

Other interesting inhabitants of the slopes are mentioned in the following list. Noteworthy among them are the handsome stinging hydroid *Lytocarpus phoeniceus*, the urchin *Echinostrephus molare*, which makes deep burrows in solid rock, and the commercial *Trochus* (*T. niloticus*), which reaches its maximum in the seaward part of the boulder zone and thence downward.

#### ANIMALS CHARACTERISTIC OF SEAWARD SLOPES AND ANCHORAGE.

(Most, if not all, the genera of corals and alcyonaria here mentioned are common to both seaward slopes and anchorage; but certain species of some of the genera are characteristic of the windward side and others of the leeward. Certain species belonging to the genera marked with an asterisk are characteristic of vertical or overhanging surfaces below the level of low water.)

##### HYDROZOA.

*Lytocarpus phoeniceus*.  
*Millepora*.

##### ALCYONARIA.

*Clavularia*.  
*Pachyclavularia*.  
*Xenia*.  
*Heteroxenia*.  
*Cespitularia*.  
*Alcyonium*.  
*Sarcophytum*.  
*Lobophytum*.  
*Sinularia*.  
*Heliopora*.  
*Lithophytum*.  
\**Dendronephthya*.  
\**Juncella*.  
\**Melitodes*.

##### ANTIPATHARIA.

\**Eucirripathes*.

##### ZOANTHINARIA.

*Palythoa*.

##### MADREPORARIA.

*Seriatopora*.  
*Pocillopora*.  
*Stylophora*.  
*Euphyllia*.  
*Orbicella*.  
*Cyphastrea*.  
*Leptastrea*.  
\**Echinopora*.  
*Galaxea*.  
*Favia*.  
*Platygyra*.  
*Coeloria*.  
*Hydnophora*.

##### MADREPORARIA—continued.

*Symphyllia*.  
*Lobophyllia*.  
*Oulophyllia*.  
*Tridacophyllia*.  
\**Merulina*.  
*Fungia*.  
*Herpetolitha*.  
*Polyphyllia*.  
*Pachyseris*.  
*Pavona*.  
*Psammocora*.  
*Diploastrea*.  
\**Dendrophyllia*.  
*Astreopora*.  
\**Turbinaria*.  
\**Montipora*.  
*Acropora*.  
*Goniopora*.  
\**Porites*.

##### POLYCHAETA.

*Spirobranchus giganteus*.

##### CRUSTACEA.

*Panulirus versicolor*.

##### MOLLUSCA.

*Trochus niloticus*.  
*Pinctada margaritifera*.  
*Tridacna crocea*.  
    ,, *derasa*.  
    ,, *fossor*.

##### ECHINODERMATA.

*Linckia laevigata*.  
*Echinostrephus molare*.  
*Stichopus chloronotus*.  
*Lamprometra gyges* and other crinoids.

## ALGAE OF THE WINDWARD SHELF AND BOULDER ZONE.

(The great majority of these species occur also in the anchorage, though some are more plentiful there than others. The three species marked with an asterisk are particularly characteristic of the windward side of the reef.)

## PHAEOPHYCEAE.

\*Sargassum cristaefolium.

\*Turbinaria ornata.

Dictyota Bartayresiana.

„ ciliata.

Padina australis.

„ Commersoni.

## CHLOROPHYCEAE.

Caulerpa racemosa.

Halimeda cuneata.

„ Opuntia.

Tuna.

\*Chlorodesmis comosa.

Bornetella nitida.

## CHLOROPHYCEAE—continued.

Dictyosphaeria favulosa.

„ sericea.

„ Versluysii.

Boodlea paradoxa.

## FLORIDEAE.

Galaxaura spp.

Laurencia botryoides.

„ papillosa.

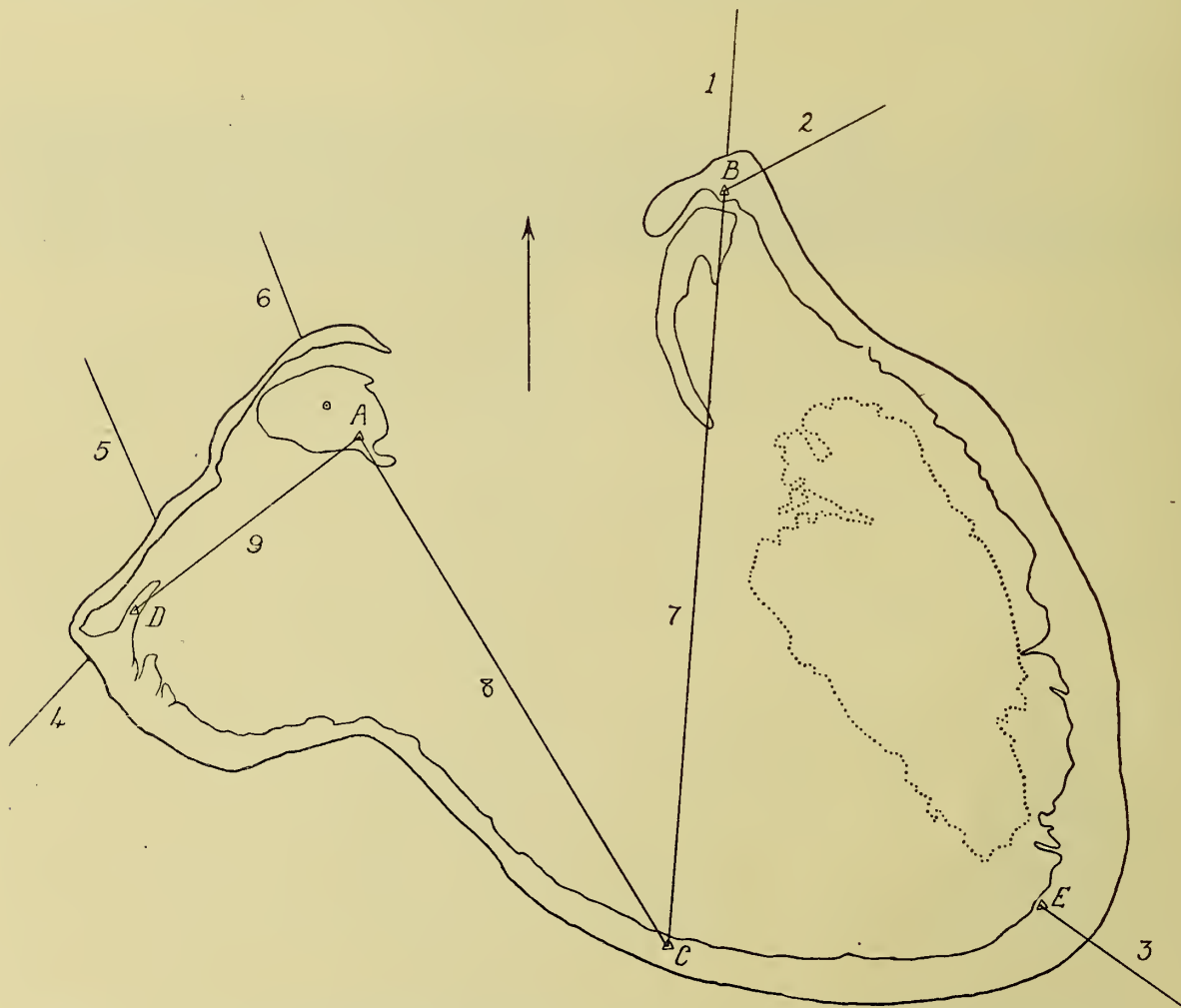
Digenea simplex.

Amphiroa fragilissima.

Melobesia.

## CYANOPHYCEAE.

Well represented.



TEXT-FIG. 11.—To show the approximate positions on the Low Isles reef of the several sections reproduced in Text-figs. 7 and 9, and of certain other sections. The letters A-E indicate the positions of beacons. Sections bear the same numbers in figs. 7, 9 and 11.

## REVIEW OF THE LOW ISLES FAUNA AND FLORA.

(By T. A. STEPHENSON.)

There are a number of points relating to groups of animals in general, which could not be brought out in the preceding regional treatment of Low Isles. So far the regions have been classified, and the animals treated as they came; if we now consider the animal groups one by one, some further relevant points will become evident. Such generalizations relating to algae as have not yet been stressed will be dealt with by Tandy in his systematic report on that group. In the case of the animals, since there will be no general report, but a large number of separate ones, it is advisable to make a short general statement here. Before leaving the plants altogether, however, I should like to enumerate a few features which are bound to strike any naturalist familiar with the intertidal regions of temperate seas, on comparing them with a coral reef.

On a typical rocky shore in a temperate region, whether it be Cornwall or Sydney, one of the most apparent features is the abundance and variety of the larger algae. Some of these inhabit high levels, some live in rock-pools, and others constitute the familiar "Laminarian zone" uncovered at spring tides, in which a dense growth of large algae of the family Laminariaceae (or in the Sydney area of their Australian counterparts, *Ecklonia*, *Sargassum*, *Cystophora*) is the dominant feature, the plants often reaching a length of several feet. On a coral reef such as Low Isles there is an immediate contrast. There is no Fucoid growth at high levels (though *Enteromorpha* may occur as on a temperate shore); the pools contain, it is true, an abundance of algae; but these are mostly not of the showy type characteristic of cooler seas, but are mossy or turf-like forms; and far from there being any Laminarian zone or comparable region, the lower levels of the shore are those in which corals are dominant and algal growth weak. The only large algae at Low Isles are brown species belonging to the genera *Sargassum*, *Cystophyllum*, *Turbinaria* and *Padina*. These make a fair growth in pools on the flat; and there is the *Sargassum*-zone already described on the windward shelf; but these features are but pale reflections of the growth in a well-stocked temperate rockpool, or in a Laminarian zone.

Another feature of coral reefs is the widespread occurrence of the nullipores (Melobesieae). These are fairly plentiful on temperate shores, but at Low Isles are almost ubiquitous in the form of thin crusts or small nodular growths, whilst on the Outer Barrier the superficial covering of Melobesieae in certain zones of the reef is so continuous and universal that much of the substratum is made pink by it. On still other reefs, of types not within our experience, the Melobesieae become massive, and may be classed among the important contributors to the bulk of the reef. At Low Isles they play a limited part in reef-formation.

Again, Low Isles is distinguished by its very extensive flora of Cyanophyceae. The abundance and variety of these dingy organisms is one of the striking features of the reef. They occur in the form of rust- or beard-like growths, as scabs on the sand, and under other manifestations, in every available type of habitat except the very driest places.

Two other sections of the algal flora are of special interest. Firstly, the vast quantities of unicellular algae or Zooxanthellae, which abound in the tissues of nearly all the reef corals as well as in those of clams, hydroids, and other animals, are responsible in great measure for the supersaturation of the water with oxygen, which occurs during certain phases of the diurnal cycle, in shallow pools containing abundant coral. This supersaturation, though relatively slight in regions such as the anchorage which are always in direct connection with the sea, is perceptible wherever coral growth is dense. It is difficult to judge the effect which this may have on the organisms exposed to it; especially as it is offset by the fact that wherever supersaturation becomes highest during the day, there will the oxygen content of the water be lowest during the night; and indeed on the flat it falls so low at night as to approach the lethal limit for fish, though not for coral. A second group of algae, interesting from a chemical point of view, are certain of the Valoniaceae (*Dictyosphaeria*, *Valonia*, etc.). Species of *Valonia* and *Halicystis* have been studied by S. C. and M. M. Brooks (1929, 1930), who have shown that the cells of these forms exercise selective accumulation of potassium, and resist the entry of sodium. The pH of the intracellular sap of *Valonia macrophyssa* under normal conditions is about 6.2, the potassium and sodium ion concentration being roughly 0.5 M. and 0.1 M. The corresponding values for sea-water are pH 8.2; potassium 0.01 M.; sodium 0.5 M.

Turning to the animals, certain general features at once appear. In the proper regions the corals and alcyonaria dominate; but apart from these the mollusca form the most extensive element in the fauna. T. Iredale collected mollusca of several hundred species at Low Isles, and a similar number at Three Isles. After these come the crustacea, with a varied and abundant series, of crabs and prawns in particular. The echinoderms, sponges and fishes are also well represented.

Another interesting point is the contrast exhibited by the rocky regions of higher level as between Low Isles and a temperate shore. On many British shores acorn-barnacles or mussels are dominant at certain levels, forming sheets so extensive as to crowd out other forms of life, apart from such species as can utilize the interstices between them. In the Sydney region, instead of these sheets of barnacles one finds an equally dense growth of the calcareous tubes of the worm *Galeolaria caespitosa*. At Low Isles, on the contrary, although acorn-barnacles are common, they never occur in anything approaching their abundance in temperate waters; and the organism which replaces them is *Ostrea mordax*, which may cover a rock so densely as to conceal it completely.

The groups of animals may now be reviewed serially, so that the relative abundance of their members, together with other points, may be indicated.

#### PROTOZOA.

An important feature here is the abundance of the large macroscopic foraminiferan *Orbitolites complanata* (Plate XIX, fig. 1). This, though more abundant in one place than another, is widespread over the reef flat. Its shells form an important element in the coarser grades of sediment on the reef, since Foraminiferan material (which must include a high proportion of *Orbitolites*) is estimated by Marshall and Orr as constituting somewhere near 20% of the sand. They also state that living flagellates, ciliates and diatoms are present among the fine detritus found in the sediment.\* It should be noted further that

\* The data given here refer to material collected in the experimental sediment-jars. The percentage of Foraminifera is a rough estimate based on a counting of fragments.

bacteria appear to play an important part in the layers of sand beneath the surface on the flat, which are everywhere more or less blackened, probably as a result of bacterial decomposition of the organic material present; and that the liberation of  $\text{CO}_2$  by bacteria in the mud of the mangrove swamp may render that mud acid, thus causing some solution of calcareous material with which it may come in contact.

#### SPONGES.

The sponge fauna is rich and interesting, and includes not only surface-living forms and typical inhabitants of pools, but also a variety of encrusting species found under slabs and boulders. The presence of the mangrove swamp provides an unusual habitat for sponges, which grow upon the roots of the *Rhizophora*, and some of which are able to penetrate the more watery parts of the swamp. Some indication has already been given (pp. 38—39) of the species which are able to flourish in the vicinity of mangroves, but a more detailed study of this question should provide results of considerable ecological interest. The only sponge of commercial value is *Euspongia irregularis* var. *pertusa*, which occurs particularly in the mangrove park. This variety is closely allied to certain West Indian forms and has been recorded from the West Indies by Hyatt, but the identification is doubtful. It is in all probability a form peculiar to Australia, if any real distinction can be made between the races of *E. irregularis*. This sponge formed the subject of experimental work by F. W. Moorhouse, described elsewhere. Another common sponge, *Spirastrella purpurea*, is remarkable for the great variation of its forms of growth, and for the fact that one of its facies resembles a colony of *Favia* so closely, in general appearance, that it might be quoted as a case of "mimicry." It is also noteworthy that sponges of certain curious cyathiform and other types common on the Outer Barrier (species of *Phyllospongia*) appear to be absent from Low Isles.

#### COELENTERATA.

(1) *Hydrozoa*.—Not many species are represented, and only two are common on the flat—*Dynamena crisioides* and *Myrionema amboinense*. The life-history of the latter was studied by E. A. Fraser and is described elsewhere in this volume. The large hydroid *Aglaophenia cupressina*, which is one of the striking features of the Outer Barrier, is apparently absent from Low Isles. Species of *Millepora* are fairly common, but occur among other corals and do not form independent reefs.

(2) *Scyphozoa*.—*Cassiopaea andromeda* is the only form recorded from Low Isles as an intertidal species.

(3) *Anthozoa*.—(a) *Alcyonaria*.—These are abundant and well represented by species as well as by individuals, and often attain a large size or cover extensive areas. It is a notable fact that nearly all the alcyonaria collected belong to the order Alcyonacea. These, with the exception of *Tubipora* and *Heliopora*, are all more or less fleshy forms (Plate XVI). This feature seems to be a characteristic of the Queensland reefs, whereas on reefs of other types, those of Florida for instance, the alcyonarian fauna consists almost entirely of Gorgonians, which give a very different facies to the reef. This distinction is so well marked at Low Isles that only two species of Gorgonians (a *Juncella* and a *Melitodes*) could be found, and these were apparently confined to shaded and overhanging surfaces on the seaward slope and formed no part of the ordinary surface-fauna. *Tubipora*, which is common on some reef-flats (*e. g.* Batt Reef), is rare at Low

Isles ; but *Heliopora* is common in the anchorage and elsewhere on the seaward slope. The alcyonaria of Low Isles, therefore, do not in the main add directly to the substance of the reef ; but through the intermediary of spicules, liberated at the time of their death, they must add very greatly to it. An interesting study of the rôle played by alcyonaria in reef-formation has been published by Cary (1918).

(b) *Ceriantharia*.—This group is represented, so far as we know, only by a single species of *Arachnanthus*, which occurs in sand.

(c) *Antipatharia*.—A species of *Eucirripathes* is fairly common on overhanging surfaces on the seaward slope.

(d) *Zoanthinaria*.—These forms, which occupy so small a space in the shore fauna of an English coast, are fairly important at Low Isles. They do not compare with the alcyonaria and madreporaria in abundance either of species or of individuals, but constitute a reasonable percentage of the coelenterate fauna. Species of *Palythoa* are the bulkiest forms, and may clothe large areas of rock.

(e) *Actiniaria*.—The group is well represented by interesting species, but many of them are of occasional occurrence. They include several of those types, characteristic of the warmer seas, which specialize in frond-like developments of tentacles, disc, or body (Plate XX, fig. 1), and also a number of perfectly ordinary species. A remarkable feature is the abundance of individuals belonging to species of large size (*Stoichactis kenti*, Plate X, fig. 1, is often a foot or 18 in. across, and the less common *Gyrostoma ramsayi* probably considerably more), but here again small species are as common as large ones. Commensalism between anemones, fish and prawns has already been mentioned (p. 47), but there is also an association fairly often seen between hermit crabs and *Calliactis miriam*.

(f) *Madreporaria*.—These are the dominant forms of life at suitable levels in the anchorage and on the seaward slopes. Certain species are able to flourish in the moats.

#### CTENOPHORA.

The only littoral form found at Low Isles was a species of *Coeloplana* taken from an alcyonarian in one of the moats.

#### TURBELLARIA.

Turbellaria of several species, including large and brightly coloured forms, are not uncommon under boulders and shingle, and form part of the fauna of the outer rampart. They may also be found among the beach sandstone.

#### NEMERTINEA.

We did not find many nemertines. The species most commonly found was a white one with longitudinal black stripes, allied to or identical with *Baseodiscus quinquelineatus*. Apart from this we can record only *Baseodiscus delineatus* and a species of *Lineus*.

#### ANNULATA.

(1) *Polychaeta*.—The most conspicuously abundant forms are *Spirobranchus gigantus*, which occurs especially in living blocks of *Porites* ; and the Polynoid *Iphione muricata*, which is common under boulders, etc. Several other species, including *Eurythoe complanata*, are more or less common, and some of these inhabit the sand. *Perinereis obfuscata* and *Platynereis polyscalma* are among the forms which may be caught by



attracting them to a light suspended over the water at night. The second of these species is a remarkable form, hitherto considered a rarity, but probably common at Low Isles. Luminous forms in great numbers were sometimes seen swimming near the cay at night, and these included *Odontosyllis hyalina* as well as the aforementioned *P. obfusca*. Certain nereidiform species are to be found in the coral conglomerate of the inner rampart, in the crevices of the beach sandstone and the boulders, and in damp places under these. Although fairly plentiful and varied, the polychaets as a whole do not appear to be among the dominant groups, except in rocky crevices, the dead bases of corals, etc.

(2) *Oligochaeta*.—The occurrence of *Pontodrilus bermudensis* in the shingle-tongues of the mangrove swamp is an interesting record.

(3) *Gephyrea*.—It has already been indicated (pp. 56. 60) that Sipunculids are plentiful both in sand and rock. The number of species is considerable and that of individuals great.

#### CRUSTACEA.

(1) *Cirripedia*.—A comment on the occurrence of acorn-barnacles has already been made on p. 70; those collected all belong to the genus *Tetraclita*. Ships'-barnacles (*e.g.* *Lepas anatifera*) are sometimes washed ashore on logs, and an interesting boring species belonging to the genus *Lithotrya* forms an element in the fauna of the coral boulders.

(2) *Isopoda*.—Apart from *Ligia australiensis* (and perhaps other species similar to or associated with it), which is common on dry shingle, members of the group are not noticeably abundant. A certain number of forms (*e.g.* species of *Cymodoce*) occur under stones and in coral crevices, and it is probable that careful dissection of habitats such as the coral platforms in the moats, would reveal a considerable number more.

(3) *Amphipoda*.—Small species are locally abundant, for instance, under shingle. Species collected belong to the genera *Hyale*, *Ceradocus*, *Maera* and *Ampithoe*.

(4) *Decapoda*.—(a) *Natantia*.—These are poorly represented in our collections, because many of them belong to the fauna of commensals and crevice-living animals of the coral platforms and the living coral which, as explained in the preface, had to be omitted from our survey; but members of the group are of frequent occurrence. Two prawns (*Crangon strenuus* and *C. ventrosus*) are fairly common on the flat, and transparent species, often with opaque bands of cream and orange, are common as commensals with both coral and anemones. There are also small species living under boulders, and in the mangrove swamp. *Periclimenes brevicarpalis* is one of the common commensals (with *Stoichactis* and *Thalassianthus*), and prawns similarly coloured were seen with living corals, including the species of *Fungia* with a tangle of tentacles 6 in. long, which remain expanded in daylight and form a refuge for the prawn. On one occasion, when diving in about 5 fathoms, a colony of *Euphyllia* some 2 ft. across was found, the coral being entirely hidden by a carpet of knobbed tentacles, among which were about two dozen of these prawns, of various sizes, all exhibiting the curious swaying motion, as if combing the tentacles, which is characteristic of them.

(b) *Palinura*.—*Panulirus versicolor* occurs in small caves and under overhanging rocks on the seaward slope below the level of low water.

(c) *Anomura*.—This group is represented by a moderate number of species, but some of them are very common. This applies particularly to some of the hermits (species of *Clibanarius*) and to the scuttling crab-like form *Petrolisthes lamarcki*.

(d) *Brachyura*.—The crabs form one of the most important elements in the fauna, including many species and innumerable individuals. They cover a wide range of form, and although they are naturally a mobile part of the population, some of them exhibit a considerable degree of response to environmental conditions, and arrange themselves distinctively with relation to the available habitats. Many of the commonest crabs belong to small and inconspicuous species, there being comparatively few large and showy forms. Their exoskeletons contribute a good deal of material to the sand of the reef. At least one species of *Cryptochirus* is of frequent occurrence in living colonies of *Favia* and *Symphyllia*.

(5) *Stomatopoda*.—Two species at least (*Gonodactylus chiragra* and *Lysiosquilla maculata*) are common, and there are other less plentiful forms.

#### ARACHNIDA.

The presence of a definitely marine spider (*Desis crosslandi*) on the flat is of interest. It occurs on the Thalamita flat and elsewhere, and is seen when slabs or boulders are turned over; in the crevices of these it makes a nest of fine mesh. It is undoubtedly submerged at high water. This species is hitherto recorded only from Zanzibar.

#### MOLLUSCA.

(1) *Amphineura*.—The Amphineuran fauna of Low Isles contrasts sharply with that of a region such as Sydney harbour. At Low Isles the number of species is small, but at least two are common, and the large *Acanthozostera gemmata* is astonishingly abundant. In Sydney harbour some 34 species belonging to 15 genera have been taken.

(2) *Gastropoda*.—The outstanding facts here are the large number of species, the vast quantity of individuals, and the great variety of conditions to which given forms have become adapted. The zonation of some of the species on the beach sandstone and the ramparts would repay detailed study, which we were unable to give to it. The gastropod fauna, far from consisting mainly of the large and brightly coloured shells so familiar in collections, consists primarily of small forms, whose shells are often dull in colour and inconspicuous, but some of which occur in countless numbers. The striking forms, though not in the majority, are nevertheless fairly well represented by certain of the larger species of cowrie (*Cypraea* and *Ovula*) and *Conus*; by the huge baler-shell (*Melo diadema*, Plate XXI, fig. 3); and by species of *Haliotis*, *Terebra*, etc. The Euthyneura include *Onchidium* in great quantity; nudibranchs of various species (among them a swimming form of magnificent coloration); a large and fairly plentiful aplysia; and the "ink-fish" *Dolabella scapula*.

(3) *Lamellibranchia*.—Here again species are numerous and individuals innumerable, and the fauna markedly subdivided among the several habitats. The boring forms (*Lithophaga*, *Gastrochaena*, *Tridacna crocea*, etc.) are among the actively destructive agencies on the reef; but some of the species, particularly the clams (*Tridacna* and *Hippopus*) are to be reckoned amongst the important suppliers of reef materials of coarse grade, since they are not only large, but also extraordinarily numerous, accounting for a colossal deposition of calcareous material from the sea-water.

(4) *Cephalopoda*.—Octopods were seen occasionally on the flat, some of them inhabiting lairs in coral debris. Squids (e. g. species of *Sepioteuthis*) were also of casual occurrence, and the shells of *Nautilus* and *Spirula* were among the shore-debris of the cay and of the adjacent mainland.

## ECHINODERMATA.

The echinoderms are well represented on the reef. Considered as a unit in reef economy they make a considerable demand upon the plant, animal and detrital food supply. They are significant also as local movers and refiners of sediment, as suppliers of abundant organic material in the form of faeces, and of skeletal material which becomes part of the sand. In this rôle they are the more effective in that they are mostly animals of a large grade of size, as well as being represented by numerous individuals.

(1) *Asteroidea*.—Of the Asteroids two species whose adults live exposed to full sunlight are common—the vivid blue *Linckia laevigata* (Plate X, fig. 2) and a similar but less plentiful brown and yellow starfish, *Nardoa pauciforis*; whilst a third exposed species, the cushion-like *Culcita novae-guineae*, is also of somewhat less frequent occurrence. Of species which habitually conceal themselves, the most notable are *Asterina (Patiriella) exigua*, which is of universal prevalence under shingle fragments and in similar places, and *Archaster typicus*, a straw-coloured starfish which lives in the Sand flat and similar areas, and may be seen in numbers moving just below or flush with the surface as the flowing tide covers the flat. The distribution of *Asterina exigua* is distinctive in that it is a typical inhabitant of the shingly areas, occurring in countless numbers on the rampart.

(2) *Echinoidea*.—Of the Echinoids the most conspicuous are the magnificent *Centrocchinus (Diadema) setosus* (Plate XX, fig. 2) and the large echinus-like *Tripneustes gratilla*; these two between them must account for the consumption of a great bulk of vegetable matter, and be a fruitful source of finely divided organic material extruded as waste. Much more plentiful than either, however, is the smaller urchin of varied coloration, *Echinometra mathaei* (Plate X, fig. 3), which is, according to Clark, probably the commonest sea-urchin in the world, and is a notorious borer; on the Outer Barrier we found it in the solid rock of the outer-moat floor.

(3) *Ophiuroidea*.—The *Ophiuroidea* are represented by several common species of somewhat different habits. Under boulders and in crevices of honeycomb-rock, especially on the flat, are to be found innumerable examples of *Ophiothrix longipeda*, a tabby-coloured species with arms which, in large specimens, may attain more than 2 ft. in length. This well-known Barrier Reef species is commonly associated with the salmon-tentacled lamellibranch *Lima tenera*. The association is not invariable (*Ophiothrix* being found frequently without *Lima*, though probably the reverse is not the case), but occurs sufficiently often to force itself upon one's notice. In the areas of honeycomb-rock, specially towards the south-east, and in the rocky-floored pools of the inner rampart, a characteristic element in the fauna is the black or dark-coloured *Ophiocoma scolopendrina*, which hides its body in an inaccessible cranny and trails some of its arms abroad. The restriction of the bulk of the population of this species (although individuals do occur under loose boulders, etc.) to areas of more or less solid rock at relatively high levels is interesting, and has been commented on by Clark with reference to its occurrence at Maer. The habitat of *O. scolopendrina* at Low Isles differs from its counterpart at Maer in that much of the rocky floor is covered by shallow water at all states of the tide; at Maer, where this is not the case, the trailing arms are withdrawn at low water. *O. longipeda* has a much more catholic distribution, and does not, in our experience, tend to trail its arms at low water, but we have seen it do so when covered by the tide.

(4) *Crinoidea*.—The echinoderm fauna of Low Isles has the interesting peculiarity that it includes no abundant Crinoid fauna between ordinary tide-marks. Clark records

the fact that on parts of the Maer Island reef (Torres Strait) Comatulids are very conspicuous and abundant, and that 21 species were found there by the Carnegie Expedition of 1913. It is not intended to state that no Crinoids can be found between tide-marks at Low Isles; a diligent search would no doubt provide a certain number of specimens; but there is no considerable population of them as at Maer, although they occur fairly freely below low water of ordinary spring tides. This state of affairs may be connected with the contrast which exists between the fauna of a reef such as Low Isles and that of reefs near or belonging to the Outer Barrier series (with which Maer ranks).

(5) *Holothuroidea*.—These are abundant, and include a number of species. Many of them fulfil an earthworm-like function in the shifting of reef-sediments. They are forms notoriously prevalent on coral reefs, and affect a variety of habitats, sometimes changing them with age, as, indeed, is the case with certain echinoderms of other groups. *Holothuria leucospilota*, for instance, lies free and exposed to direct sunlight when adult; but when young it appears to prefer sheltered shady places and may be found under the shingle of the rampart. Of the species which live in sheltered places when adult, some live under boulders and others in sand, a variety of small and young forms occurring under the shingle of the rampart. It has recently been shown by Baker (1929) that on a reef which he visited in the New Hebrides, certain Holothurians exhibit a very distinct zonation.

#### POLYZOA.

These appear to be rather poorly represented in the Low Isles fauna, being less abundant than on many temperate shores. The most interesting form is the finely branched coral-like species *Retepora graeffei*.

#### BRACHIOPODA.

So far as we are aware these are absent from Low Isles; but a species of *Lingula* is very plentiful in Mission Bay, Cape Grafton on the mainland some 35 miles to the southward.

#### ASCIDIACEA.

The ascidian fauna is curious in that individuals belonging to simple species were rarely seen. Compound ascidians, on the other hand, are very abundant, though in individuals rather than in species. The vivid blue or green *Diplosoma virens* is very widespread, and sometimes present in countless numbers. The white *Didemnum candidum* and a pink form probably belonging to the same species are also very common in a variety of places, and another species of this genus (*D. psammatodes* var. *skeati*) is fairly plentiful.

#### ENTEROPNEUSTA.

Only the two species mentioned previously (p. 56) were found, but both of these are abundant. Enteropneusts appear to form a characteristic element in the fauna of coral reefs, amongst which they are widely distributed. An interesting comment on them is made, for instance, by Gardiner in his reports on the Maldivé and Laccadive Archipelagoes (vol. i, pp. 47, 340).

## FISHES.

A short account of the Low Isles fishes has been published by G. P. Whitley (1929).

On the reef flat several fish of moderate size are common. One is a very sleepy dog-fish, easily captured, and with large eye-like markings on its sides (*Chiloscyllium ocellatum*). Another is a handsome sting-ray, reddish brown with bright blue spots (*Taeniura lymma halgani*). A dark grey ray (*Himantura granulata*) occurs in the mangrove swamp. A really dangerous inhabitant of the reef, the stonefish *Synanceja horrida*, was taken on several occasions. A toadfish (*Tetrodon hispidus*) is fairly common, and a coffer-fish less so. Of the smaller fish, shoals are of frequent occurrence in moats (*e. g. Pranesus ogilbyi*), or around mangrove-roots (*e. g. Pseudomugil signifer*), and a number of species are commensal with coral. Of the large off-shore fish the mackerel-like *Scomberomorus commerson* is one of the local food-fishes. Sharks of large size (8–12 ft.) are apparently not very plentiful about the reef, though seen from time to time. They sometimes came very close inshore, and might be found, for instance, in the mangrove park at a state of the tide which hardly provided them with sufficient depth of water for movement. Rays of large size were sometimes seen leaping from the water near the shore, but close views of such species were obtained only on Batt reef, where they measured as much as 6 or 8 ft. across. Whitley states that the fishes of the mangrove area are, broadly speaking, “of an entirely different faunal facies from the coral fishes.” A note on the coral fishes will be found on p. 66.

## REPTILES.

Geckos live on the cay and in parts of the mangrove swamp. Sea snakes were sometimes seen both on the reef flat and out at sea, but were not common.

## BIRDS.

The Low Isles reef is the territory of a pair of sea eagles (probably *Cuncuma leucogaster*), which nest in a tall tree in the mangrove swamp. The swamp is also the roosting-place of innumerable Torres Strait pigeons (*Myristicivora bicolor* subspecies *spilorrhoea*) during certain months of the year, and many of these fly to the mainland each day and to Low Isles each night. Grey and white herons (probably *Demicregretta sacra*) frequent the reef, and many of these fly out to Batt Reef as the tide ebbs, arriving there as it begins to uncover. The cay is inhabited by other smaller birds, and migrants are sometimes killed by collision with the lighthouse.

## ORIGIN OF THE LOW ISLES FAUNA.

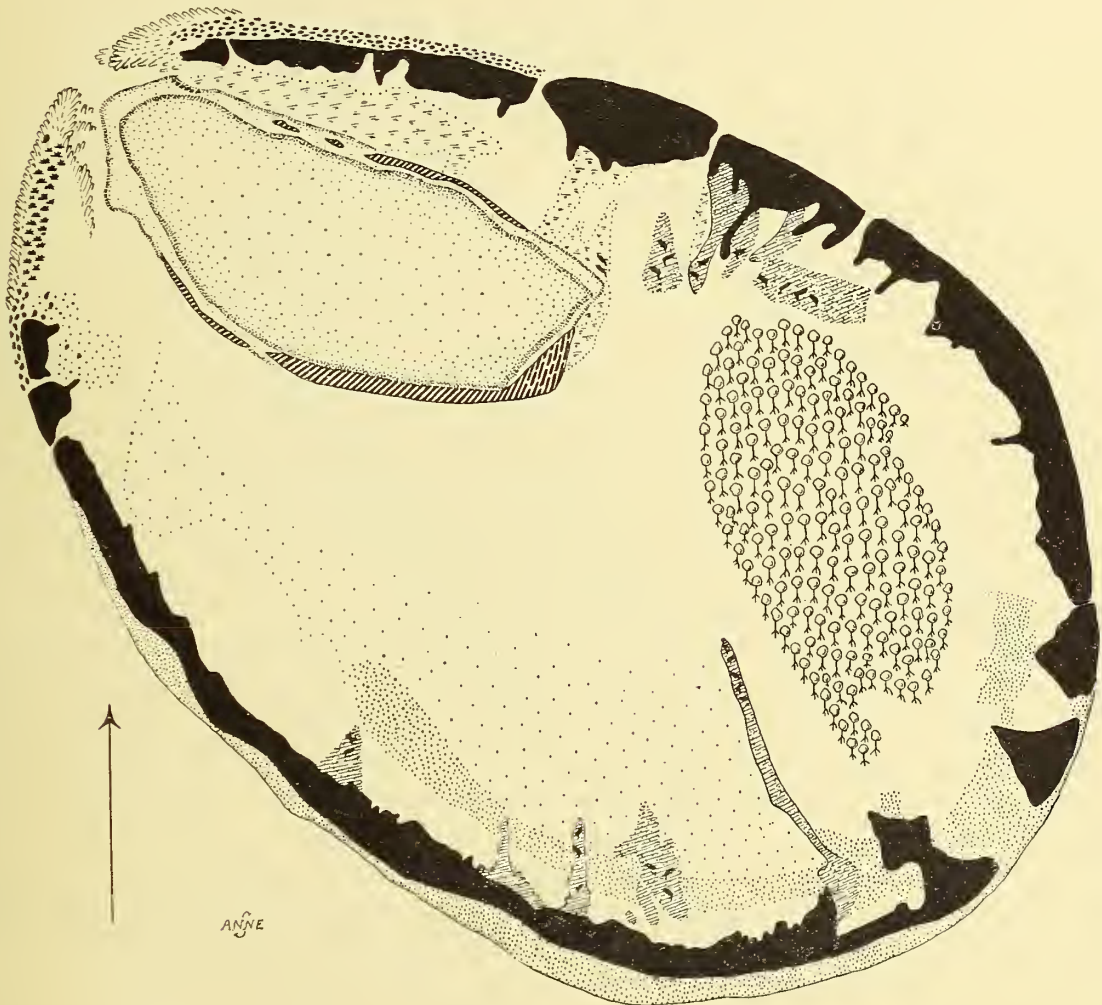
We hoped to make an analysis of the species represented in the Low Isles fauna, tabulating their known geographical distribution so that some idea of the composition and origin of the fauna might be gained. Since the species collected number many hundreds, this has proved too great an undertaking, and has been abandoned. It is possible, however, to give one illustration which will give an indication of the state of affairs, and which would probably prove to be of wide application.

The echinoderms of Low Isles include a number of more or less common representatives not yet mentioned in this report, some of which, though not particularly prevalent at Low Isles, are common elsewhere in the Barrier region; these include *Asterope carinifera*, *Echinaster luzonicus*, *Orcaster nodosus*, *Iconaster longimanus*, *Ophiarthrum pictum*, *Ophiolepis superba*, *Ophiocoma brevipipes* var. *variegata*, *Ophiarachnella gorgonia*, *Ophiactis savignyi* and *Holothuria marmorata*.



TEXT-FIG. 12.—Diagrammatic analysis of the Low Isles reef, for comparison with the Three Isles reef, as represented in Text-fig. 13. The conventions used in the two figures are the same. The figures are an attempt to compare those areas in the two reefs which correspond ecologically; the terms used are therefore not necessarily intended to imply *morphological* correspondence between the parts compared, although a good deal of such correspondence is involved. Regions not strictly comparable ecologically are omitted; some of these are compared in Text-fig. 15. The mangrove area is represented by a uniform convention in both figures, as a guide to the eye; actually it contains glades and shingle tongues in both cases, but since the details of these are not known for Three Isles, the two reefs cannot be compared in this sense. The details for Low Isles are shown in Plate I.

If we take the species just enumerated, and add them to those mentioned elsewhere in this report, we obtain a series from which 33 species may be chosen to represent the echinoderm fauna of Low Isles. The existence of Lyman Clark's lucid and excellent monograph on the Echinoderm Fauna of Torres Strait makes it possible to analyse this group of species. Of the total of 33, 23 at least (probably more) are Indo-Pacific forms of



TEXT-FIG. 13.—Diagrammatic analysis of the Three Isles reef for comparison with Text-fig. 12.

greater or lesser range, whilst 6 belong to the East Indies, the Pacific, or both. One at least, probably two, are pan-tropical. Further, 8 of them are species listed by Clark as forms of very wide range, 5 as species of tropical Australian range, 4 as particularly characteristic of the Thursday Island area, and 14 as characteristic of the Barrier Reef area (the echinoderm fauna of which is in the main markedly different from that of the Thursday Island region). Clearly, then, the Low Isles fauna is predominantly Indo-Pacific as regards its echinoderms, and this undoubtedly applies in other groups, if not generally.

## COMPARISON OF THE ECOLOGY OF OTHER REEFS WITH THAT OF LOW ISLES.

(By T. A. and ANNE STEPHENSON.)

### I. THREE ISLES.

(Text-figs. 13-15 ; Plates II and XXII ; Plate XXVI, fig. 1.)

The survey of this reef was carried out by M. A. Spender and Anne Stephenson. The biology was studied by J. S. Colman, T. Iredale and T. A. Stephenson. The time thus occupied was a week, at the period of new-moon spring tides, in May, 1929. The survey, though brief, came towards the end of our careful study of Low Isles, so that we were able to make a satisfactory comparison in a short time.

Our notes on the physiography, fauna and flora of Three Isles are of considerable bulk, but there is no need to publish them *in extenso*, since the principal fact which they demonstrate is a very close similarity between Three Isles and Low Isles. A brief account of the structure of Three Isles (p. 27) has already been given, and this, together with the coloured maps and Text-figs. 12 to 15, bring out the points of resemblance and of contrast between the two reefs. It remains, therefore, only to mention certain features of particular interest connected with Three Isles.

The ecological associations of Three Isles are exactly similar in principle to those of Low Isles. A complete list of species from Three Isles would be a question of repeating the Low Isles list, with a certain proportion of alterations. An extensive list is available only in the case of the mollusca (to be reported upon by Iredale), but numerous shorter lists compiled in the field show the same common organisms as at Low Isles. Some *differences* are as follows :

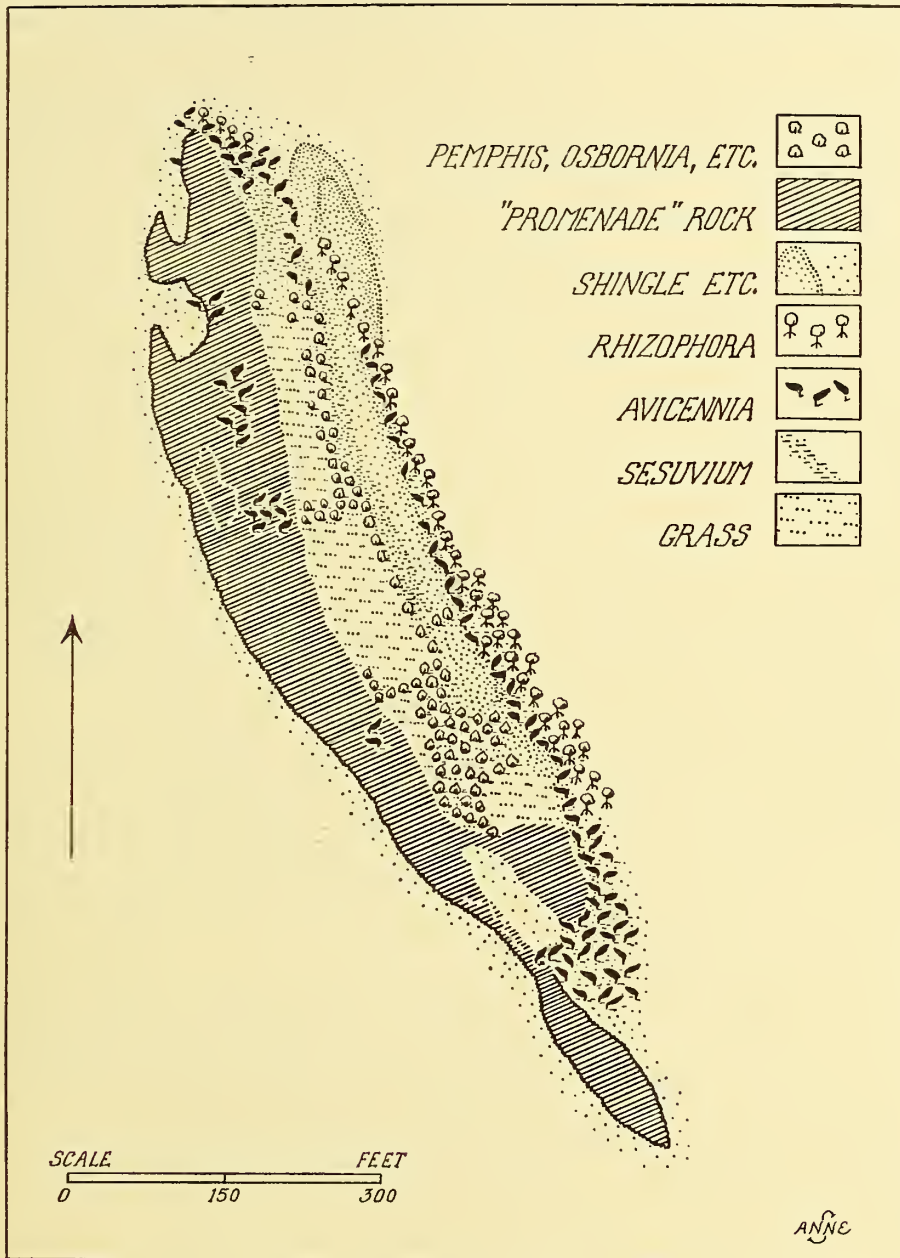
**THE CAY.**—The flora of the Three Isles cay probably gives a better idea of the flora characteristic of cays than that of the Low Isles cay, since it is not inhabited by light-keepers. Much of it had been burnt off previous to our visit ; but it includes a number of interesting species, notably the beautiful pink-flowered *Josephinia grandiflora*, a form typical of such situations, which was represented in the collections made by Banks at Lizard Island in 1770 and by Macgillivray at Three Isles in 1848. The trees are *Pandanus*, *Cocos*, *Casuarina*, *Terminalia*, etc.

There is more beach sandstone round the cay at Three Isles than at Low Isles, and it has an interesting zonation of molluscan species. According to Iredale the following species occur on all the patches of sandstone. The zonation from above downwards runs—*Melarhappe coccinea*, *Tectarius malaccanus*, *Melarhappe undulata*, *Planaxis sulcatus*, *Siphonaria*. Four species of *Nerita* (*chamaeleon*, *polita*, *plicata*, *albicilla*) occur without distinct arrangement throughout the above zones.

**THE FLAT.**—Three Isles has no mangrove park. Between the mangrove swamp and the very long shingle-spit outside its western border lies an interesting pool containing flat-topped platforms of massive corals (*Porites*, *Favia*, *Symphyllia*), together with



some platforms of *Heliopora* and *Pavona*, and a thoroughly interesting population of other creatures. This pool is rather similar to the "Porites pond" of Low Isles, and its



TEXT-FIG. 14.—Diagrammatic representation of the Third Island at Three Isles, showing the general distribution of zones of vegetation upon it.

population is that of a well-stocked moat. The flat just outside the swamp, to the north of this pool, is mostly sandy, with a thin colonization of *Thalassia*.

The tiger-cowrie (*Cypraea tigris*) is very common on the flat at Three Isles. This was probably equally common at Low Isles in the past, but has been so much sought after by lighthouse-keepers and visitors that it is now scarce.

CASUARINA SPIT AND THE DUNE present an interesting flora. Casuarina spit is covered by a coppice, including a variety of shrubs and flowering plants apart from the casuarinas. The dune (Plate XXII, fig. 3) varies from place to place; part of it is covered by woodland, part by vegetation somewhat resembling that of heath-country. *Pandanus* is among the trees of the area.

THE THIRD ISLAND (Text-fig. 14; Plate XXVI, fig. 1) gives an interesting example of plant-zonation. Its bands of shingle and debris are colonized by *Sesuvium*, grass, *Pemphis acidula*, *Osbornia octodonta*, etc.; along its eastern margin lies a belt of *Avicennia*, and between this and the flat a strip of *Rhizophora*.

THE PROMENADES (Plate XXII, figs. 1 and 2) have a fauna and flora of their own, distinctive features of which are the crab *Grapsus strigosus*, which clatters about the rocks; and the periwinkles *Nerita plicata* and *costata*. There is *Sesuvium* on top of the high promenade outside the mangrove swamp, among other places.

THE ANCHORAGE AND ADJACENT REGIONS.—A finishing touch is given to the ecological correspondence between Three Isles and Low Isles by the arrangement of areas in the anchorage. At Three Isles there is an area of slightly higher level than the rest (corresponding to the area A1 at Low Isles, described on p. 62), on which *Acropora pulchra* is conspicuous. The other anchorage reefs have a fauna comparable to that of A2, etc., at Low Isles. These points are indicated in Text-figs. 12 and 13.\* The growth of coral in the Three Isles anchorage is particularly clean and fresh, and in May, 1929, was not at all infested by Cyanophycean beards, such as were smothering the Low Isles coral at the same time.

A region at Three Isles which has no exact counterpart at Low Isles is to be found between the anchorage and the flat. It is like a much more extensive version of the small area at Low Isles where the northern moat opens on to the anchorage. It is a wide stretch of pools and platforms of *Acropora*, massive *Porites* and *Montipora ramosa*, supporting a rich fauna, and intermediate in its conditions of life between a moat and the anchorage—a moat-like area more directly in contact with the open sea and, when not submerged, with water continually streaming through it.

Only one common coral species was noted as a form not familiar to us at Low Isles. This was an important form ecologically—a species of *Acropora* (*A. brueggemanni*) occurring in quantity on the part of the flat adjacent to the anchorage, and making platforms like those of *A. hebes* at Low Isles (the latter species was also present).

Certain alcyonaria are common in the anchorage which are not recorded from Low Isles—these include *Isis hippuris*, *Cespitularia multipinnata*, and another species of *Cespitularia*.

## II. YONGE REEF.

(Text-fig. 5; Plate XVII, fig. 2; Plates XXIII and XXIV; Plate XXVI, fig. 4.)

During the new-moon tides of June, 1929, we established a base on Lizard Island, and from there Yonge Reef was visited on five successive days. A short visit was also paid to Ribbon Reef on 4th June. These two reefs have been named since our visit: the name Yonge Reef was proposed by the Admiralty; the name Ribbon Reef was suggested by us and confirmed by the Admiralty. The work on Yonge Reef was carried out by M. A. Spender, Anne Stephenson, E. A. Fraser, S. M. Manton and T. A. Stephenson. An instrumental survey was not possible in this case.

\* *Acropora pulchra* occurs in the areas marked "region of special madreporæ," in these figures.

In the fauna and flora of Yonge Reef we were presented with a new set of problems, offering very little basis for comparison with Low Isles and Three Isles. The coral and alcyonarian species were unlike those with which we had become familiar, and although closer study showed that many of them represented modified growth-forms of Low Isles species, or forms which in the latter place are limited to the windward side, others were actually new, and everything looked a little different. This, I believe, is a common experience in turning from one reef to another, but it is important and worth careful investigation, because a solution of the problem presented would go a long way towards elucidating the distribution and evolution of marine species in general. It is probably only partly correlated with the differences in environment between one reef and another.

At Yonge Reef the complications presented by the occurrence of ramparts, mangroves, and a sandy reef-flat, do not exist. In their place the question of the relationship of organisms to Pacific breakers becomes insistent; and there are new factors involved in connection with the curious series of band-like zones already described (p. 32) which make up the seaward side of the reef. The meaning of the exact configuration of these zones it is impossible to interpret accurately in the present state of our knowledge. We can therefore only describe the life of the zones, and leave the interpretation to the future. The description starts at the Pacific border and works inwards.

THE OUTER RIDGE (Plate XXIII, fig. 2).—Coral grows luxuriantly on this ridge.† The corals include massive species, some of them growing to large size, and species of *Acropora* of certain styles of growth. These latter may form wide dish-like brackets or expansions (*A. hyacinthus*), encrusting sheets yards in extent (*A. palifera*), systems of heavy branches closely applied to the substratum (*A. decipiens*); or may consist of very short massive cones united to a firm foundation (*A. gemmifera*). Apart from these more or less solid forms, a totally different species (*A. delicatula*), occurring particularly on the sides of clefts, makes small rounded bushes of branches so slender and brittle that an entire specimen can with difficulty be obtained—yet this form can withstand the breakers.\*

THE OUTER MOAT (Plate XXIII, fig. 1).—The coral here is most profuse near the outer ridge, where it occurs on large rocky prominences intersected by deep pools and crevasses. Little of this becomes fully exposed even at low water, and the water of the moat is normally agitated; it can rarely, if ever, approach the still conditions of a moat at Low Isles. The corals include the several growth-forms already mentioned for the outer ridge, and a variety of others beside. Conspicuous organisms other than corals are a large and handsome yellowish-brown hydroid (*Aglaophenia cupressina*), which is notably abundant, a common sponge of Heliopora-like growth (*Phyllospongia ridleyi*), *Spirobranchus giganteus* buried in coral, and various alcyonaria. There are also clams, gastropods, hermits, compound ascidians and encrusting sponges. As the water becomes shallower towards the reef-crest the floor becomes smooth, the coral more and more scattered, and the sea-urchins *Echinostrephus molare* and *Echinometra mathaei*, abundant. Both are borers, the former making deep rounded holes, sometimes as many as six to the square foot.

A primary feature of Yonge Reef is the heavy incrustation of nullipores. Even the

\* The well-known views of Wood-Jones on the relationship between growth-form and environment in corals will be discussed in another paper.

† The upper part of the actual Pacific slope of the reef also appears to support a rich growth of living coral, since the refracted image of such a growth can be seen in the arch of the breakers before they disintegrate.

gastropods are usually overgrown by them. All the zones from the Pacific to the boulder zone consist of solid rock swept clear of loose debris, and for the most part so generally encrusted with nullipores that the prevailing colour of the substratum is a purplish pink. This is misleading, because the rock consists of coral and the nullipores are only a veneer; but it renders the landscape to leeward incomparably beautiful, for it has a pink foreground, with the brilliant blues and greens of shallow water over white sand behind it. A factor of importance connected with Yonge Reef is that the floor of its leeward side consists of very clean, rather coarse white sand. No mud or greyish sand, like that of Low Isles, was seen, and the water is very clear.

THE REEF CREST (Plate XXIII, figs. 1, 3 and 4).—This slopes upward from the outer moat to a summit-zone. Species of *Acropora* dominate, including *A. hebes*, *pulchra squamosa* and *gemmifera*. The two former make low bushy growths, the latter cyathiform structures with a stout stalk and short branches on top. *A. gemmifera* is particularly characteristic of Yonge Reef, and has short branches, which exhibit varying degrees of reduction to thumb-like or conical processes (Plate XXIV, fig. 2). Besides these are corals belonging to other genera, together with alcyonaria (including *Tubipora* as well as soft forms) and other organisms. Among the latter the most conspicuous are *Aglaophenia cupressina* and *Linckia guildingii*, the latter being a fawn-coloured starfish similar to the blue *L. laevigata* of Low Isles, which is also present. *Phyllospongia ridleyi* and a grey-green Zoanthid are also very common here. Where boulders occur there is a good growth of underside sponges, compound ascidians (including *Chorizocarpa sydneyensis*), small spider-crabs, oysters, *Sertularia*, etc. In shallow pools a squilla is common, and clams, gastropods, hermits, *Palythoa*, *Stichopus chloronotus* and other holothurians are present. A characteristic alga is *Chlorodesmis comosa*, and there are small amounts of *Halimeda* and *Caulerpa*.

The reef-crest varies to some extent from one place to another. In many places (Plate XXIII, fig. 3) it is very bare, in others (Plate XXIII, fig. 4) there is a considerable growth of coral of a certain type. The dominant species of *Acropora* vary to some extent. *A. gemmifera* is usually plentiful; sometimes patches of *A. hebes* and *pulchra* occur; elsewhere *A. squamosa* becomes dominant. At its northern end the reef-crest loses height and fans out, becoming covered by a good growth of *Favias*. At the southern end it also slopes downward, and terminates in a peculiarly bare zone with a poor growth of *Melobesieae*, but with a turf of soft algae; there is hardly any coral here. The reef-crest appears to have caverns beneath it, since water wells up through holes in its surface.

Connected with the ends of the reef-crest are some curious areas (Text-fig. 5), which present variations upon the zonation of the principal length of the reef, as follows:

A. *Madrepore Fields*.—Immediately to westward of the southern termination of the reef-crest lies an area (Plate XXVI, fig. 4) covered by a luxuriant growth of *Acropora hebes*. *Acropora gemmifera* is a subsidiary form here, and other corals are present in smaller numbers. At the northern end of the reef is a second field of *A. hebes*, this time to seaward of the end of the reef-crest; and there the branches of the madrepores are shorter and thicker than in the southern field.

B. *Intermediate Zones*.—At the southern end of the reef there are curious areas, lower in level than the reef-crest, and situated to seaward of it, in which the floor is horizontal instead of sloping. A similar area occurs at the northern end.

THE INNER MOAT (Plate XXIII, fig. 4).—Here the bottom is still rocky, but

irregular, and such boulders as occur are mostly cemented to the floor. Coral growth is fairly strong, often in scattered clumps. The fauna and flora reflect those of the outer moat, but the general effect is often somewhat impoverished. The inner moat is well marked in places, but sometimes, and perhaps over considerable stretches, the transition from reef-crest to boulder zone is gradual, a distinct moat being absent. This occurs notably in two areas of rather distinctive character, one at either end of the reef, which are labelled "sub-terminal areas" in Text-fig. 5.

THE BOULDER ZONE (Plate XXIII, fig. 4).—Here for the first time loose boulders and other debris are encountered in some quantity, and sand also appears in certain of the pools. Corals are scattered about the rocks and in the pools, and are similar to those of the inner moat, though somewhat less frequent. There is a good fauna beneath the boulders. There are also thick patches of *Caulerpa* and *Halimeda*, a great deal of *Spirobranchus* in the coral, some clams (*T. crocea* and *T. fossor*), *Linckia laevigata* and *gouldingii*, *Echinometra mathaei*, etc. At the southern end of the reef an expansion of the boulder zone ("southern boulder area" of Text-fig. 5) comes into contact with the outer moat.

THE ANCHORAGE CORAL ZONE.—This zone has been so named because it resembles, both in structure and fauna, the reefs found in the anchorage at Low Isles. The association of corals which grow on the leeward sides of reefs in the shallower water, on the tops and sides of rugged masses of rock with sandy pools between, constitutes a distinguishable series of species and growth-forms, to which we referred during our work as the "anchorage-coral" association. This community will be defined more closely in a later report, and will be contrasted with other groups characteristic of different habitats; for the moment it will be enough to say that it is distinct from the association characteristic of the windward slopes of reefs at comparable levels.

In this zone the blocks of dead coral are richly overgrown by living forms in great variety, amongst which stagshorns and other species of *Acropora* predominate. *Acropora palifera* is one of the common species, and this, under several growth-forms (some of which may be distinct species) is present in most parts of the reef. It is a massive, encrusting or lobed form unlike the other species of the genus. The pools abound in brightly coloured fish. In the deeps there often flourish great clumps of staghorn coral, directly on the sand, unsupported by any considerable piece of rock or other solid foundation. Among the coral are giant clams (*Tridacna derasa* and *T. elongata*), as well as the smaller species. *Hippopus* is present, but is scarce on this reef. There are also crinoids, and algae such as *Chlorodesmis* and *Halimeda*.

THE ZONE OF CORAL HEADS (Plate XXIV, fig. 2).—The coral heads, many of them very large, are mostly well spaced, with a sandy floor between them, bare but for odd boulders and patches of staghorn coral. Their tops emerge 2–3 ft. at low water of extreme tides, the average emergence being about 1 ft. Some of them are completely covered across the top by a very rich and dense growth of living coral; other have the tops partly dead, with loose shingle, etc. The incrustation of the dead parts with nullipores is very extensive, and these sometimes veneer large masses of coral, which appear to be made of solid nullipores until broken. The colour of these nullipores was often pure white; this probably means that they were dead. A very considerable proportion (some 10% to 20%) of the living corals exposed during this set of tides were killed by the sun, their clean white skeletons advertising the date of their death with some precision, since the skeleton becomes brown and encrusted within a few days of death. The dominant corals of the

tops of the coral-heads are species of *Acropora*, particularly bracket-like forms and species with short thick branches ; but many other subsidiary species occur. The growth is well illustrated by Plate XXIV, fig. 2.

THE FAUNA AND FLORA OF THE REEF AS A WHOLE.—The following list of organisms will give some idea of the general population of the reef.

FAUNA AND FLORA OF YONGE REEF.

PORIFERA.

- Stelletta purpurea*.
- Phyllospongia foliascens*.
- "    *ridleyi*.
- Various other species, both surface and concealed forms.

HYDROZOA.

- Aglaophenia cupressina*.
- Sertularia*.
- Millepora*.

ALCYONARIA.

- Tubipora*.
- Xenia*.
- Sarcophytum*.
- Lobophytum*.
- Sinularia*.
- Heliopora*.
- Lithophytum arboreum*.
- "    *digitatum*.

ZOANTHINARIA.

- Palythoa* and other forms.

MADREPORARIA.

- Seriatopora*.
- Pocillopora*.
- Stylophora*.
- Euphyllia*.
- Cyphastrea*.
- Echinopora*.
- Galaxea*.
- Favia*.
- Platygyra*.
- Coeloria*.
- Hydnophora*.
- Symphyllia*.
- Lobophyllia*.
- Pavona*.
- Astreopora*.
- Montipora*.
- Acropora*.
- Goniopora*.
- Porites*.

POLYCHAETA.

- Spirobranchus giganteus*.

BRACHYURA.

- Charybdis orientalis*.
- Actaea tomentosa*.
- Zozymus aeneus*.
- Trapezia ferruginea*
- "    (commensal with *Stylophora*).
- Percnon abbreviatus*.

GASTROPODA.

- Trochus*.
- Clava vertagus*.
- Cypraea lynx*.
- "    *moneta*.
- Pterocera*.
- Thais armigera*.
- Drupa cornus*.
- "    *ricinus*.
- "    *rubus-caesius*.
- Latirus smaragdulus*.
- Conus lividus*.
- "    *marmoreus*.
- "    *striatus*.
- "    *vexillum*.

LAMELLIBRANCHIA.

- Tridacna crocea*.
- "    *derasa*.
- "    *elongata*.
- "    *fossor*.
- Hippopus hippopus*.

ECHINODERMATA.

- Linckia guildingii*.
- "    *laevigata*.
- Nardoa pauciforis*.
- Echinometra mathaei*.
- Echinostrephus molare*.
- Stichopus chloronotus* and other *Holothurians*.
- Crinoids*.

ASCIDIACEA.

- Chorizocarpa sydneyensis*.
- Botryllus magnicoecus*.

ALGAE.

- Caulerpa* and *Halimeda* present.
- Chlorodesmis comosa* abundant.
- Melobesia* dominant.

## III. LIZARD ISLAND.

(Text-fig. 6 ; Plate XXV ; Plate XXVI, fig. 3.)

We camped on this island from 1st to 12th June, 1929. On four of these days examinations were made of some of the reefs surrounding the island.

These reefs are not all of the same type. They form a curious series and would repay further study. In Text-fig. 6 the principal reef-areas are represented in solid black. From this figure it may be seen that a considerable part of the coast-line possesses a narrow band of fringing reef ; that a more extensive system of reefs occupies the space between Lizard Island and its southern satellites Newt and Iguana Islands ; and that in addition to these there are small reef-patches here and there. It may also be seen that a shoal flanks the western side of the system of islands.

THE FRINGING REEFS.—These are narrow band-like reefs adjacent to the coast. They are seen to advantage from the slopes of the mountain, their form, extent and abrupt seaward edges being clearly defined against the white sandy bottom. One of these reefs was examined. Inshore were a few granite boulders, with some coral debris and shingle partly masked by a dense growth of *Sarcophytum*, *Lobophytum* and *Sinularia*. The water even inshore was about a foot deep at this tide (9th June), many of the alcyonaria projecting. Proceeding towards the edge of the reef the water deepens, and about 10–15 yards from the shore there are large masses of living *Porites*, frequently a couple of yards in diameter, with pools and channels between. These masses continue to the edge of the reef, which lies some 50 yards from the shore, and descends rapidly to deep water, in irregular steps ; and towards the margin the pools and crevices are of considerable depth. Outside the reef-edge the bottom is clean sand. On and between the larger coral masses flourishes a rich and varied growth of other corals and alcyonaria, including fields of *Sinularia flexibilis*. This fauna resembles that described below (p. 88) for one of the isolated reef-patches, and includes, in addition to the forms there mentioned, species of *Oulophyllia*, *Tridacophyllia*, *Pachyseris*, *Pavona*, *Echinopora*, *Galaxea*, *Psammocora*, lobed and foliose *Porites* ; *Stichopus chloronotus* and *Gyrostoma ramsayi*.

This reef, which is probably typical of the fringing reefs of the island, appears to be a young reef, with no reef-flat, still narrow, and consisting mainly of living coral, with a predominance of massive *Porites*. The escarpment which forms the seaward face is made of tiers of living colonies of this coral.

THE REEF PATCHES.—The nature of the reefs other than straightforward fringing reefs is indicated in Plate XXV and Plate XXVI, fig. 3. Plate XXV represents the view to southward from a height of some 1100 ft. near the summit of Lizard Island. In the foreground the coast and foothills of the island are seen ; in the middle distance, the satellites, Newt and Iguana Islands ; and between these and the foreground, a system of reefs. Between Iguana and Newt Islands, and between the latter and Lizard Island, this reef-system has a distinct edge and constitutes a sort of miniature barrier-reef upon which there is surf in ordinary south-easterly weather. This barrier encloses a deep pool (to the left of the figure), a practicable anchorage for small craft, with an entry which lies just outside the picture. Westward of the pool, between Iguana and Lizard Islands, lies a sandy shoal of complicated outline and very variable in level. Upon this occur numerous reef-patches, some of them adjacent to the shore of one or other of the islands, others quite isolated. In Text-fig. 6 this latter area is represented very conventionally ;

the two black masses actually represent groups of reef-patches, and many individual patches are omitted. Some of the latter are shown in Plate XXVI, fig. 3. The sea floor to westward of Lizard Island, as far as the eye can see from the slopes of the mountain, is sandy, with isolated reef-patches, some of them at a considerable distance from the shore. The distant reefs in Plate XXV are not reef-patches, but are large reefs belonging to the "inner series"—Eagle Island, M Reef and L Reef. The relation of these to Lizard Island and to the mainland is indicated in Text-fig. 1.

Three of the isolated reef-patches were examined, and one of these (lying to the west of Iguana Island in Plate XXV) will be described. It is a reef separated by some distance from any shore, and surrounded on all sides by sand. The shape is roughly triangular, the apex to windward (S.E.). The reef is made of dead boulders and masses of coral with sand between, and the surface is very irregular and full of complex holes and crevices. The edges are abrupt, about 6 ft. deep on the windward side. The general surface of the reef (apart from exceptional prominences) was about a foot below the level of low water at the tide of 3rd June; at an extreme tide there would be some exposure.

The whole reef is covered with a rich and healthy growth of coral and alcyonaria, resembling that of the Low Isles anchorage, but including some elements characteristic of more exposed situations. Fleshy alcyonaria are plentiful; *Acropora* is represented by about twelve species, including *A. palmifera* and cyathiform, stagshorn, and bush-like species; and *Montipora* by both branched and foliose forms. Among the corals are other creatures, especially giant clams, some of them 3 ft. long or more. The largest species is apparently identical with *T. derasa*, the other with *T. elongata*. Smaller species are also present. Further details of the fauna are given in the list at the foot of this page.

The interest of the reef lies in the picture which it presents of the structure and fauna of an isolated reef-patch growing up from a sandy floor. The conditions described probably resemble those which prevail on any comparable reef before it has acquired a reef-flat or a modified surface which restricts or abolishes the growth of coral on top of it. A second reef-patch which we examined, a little to westward of the one described, seemed to have reached a slightly more advanced condition, since it had a sort of embryonic reef-flat of boulders, sand and shingle, with a slight stony bank at one side, exposed at low water. Here the growth of living coral was restricted on top of the reef, but was very rich down the steep sides. Connected with this reef was a notable mass of coral many feet deep, square yards of which were covered by a living colony of *Diploastrea heliopora*.

#### FAUNA OF REEF-PATCH DESCRIBED ABOVE.

##### HYDROZOA.

*Aglaophenia cupressina*.

##### ALCYONARIA.

*Sarcophytum*.

*Lobophytum*.

*Sinularia* (*S. flexibilis* and other species).

*Isis hippuris*.

##### ZOANTHINARIA.

*Palythoa*.

##### MADREPORARIA.

Discosomidae.

Seriatopora.

Pocillopora.

##### MADREPORARIA—continued.

*Stylophora*.

*Favia*.

*Platygyra*.

*Coeloria*.

*Symphyllia*.

*Lobophyllia*.

*Merulina*.

*Fungia*.

*Herpetolitha*.

*Polyphyllia*.

*Turbinaria* (massive and foliose species).

*Montipora*.



MADREPORARIA—*continued.*

Acropora.

Goniopora.

Porites (massive).

## MOLLUSCA.

Tridacna crocea.

,, derasa.

MOLLUSCA—*continued.*

Tridacna elongata.

,, fossor.

## ECHINODERMATA.

Linckia laevigata.

Echinometra mathaei.

Crinoids.

## IV. BATT REEF.

(Text-fig. 4 ; Plate XXVI, fig. 2.)

This reef was visited on a number of occasions from Low Isles. The area best known to us is the north-western part of the reef, somewhat south of its northern extremity, and in one of the pools in this region a small area was surveyed in detail. Apart from this, some examination was made by Tandy across the northern end of the reef, and one long trip was made by several of us in a dinghy across the sand-flat and down the length of the reef, ending at a point on the seaward edge near the south-east corner. A landing was also made on a reef-patch between Batt Reef and Tongue Reef. Our knowledge of Batt Reef is summarized in Text-fig. 4.

The only primary growth of living coral to be found on this reef occurs on its seaward slopes. The reef-patch just mentioned bears a rich and flourishing coral fauna.

The enormous central sand-flat has its own internal fauna, but the surface is almost bare for miles. Passing over it in a dinghy just before or after the period of low water, one sees a great population of fish, including shoals of large species, and rays 6 or 8 ft. across. The surface of the sand is populated chiefly by sand-binding plants, amongst which species of *Caulerpa* often form trailers many yards in length. *Thalassia* and *Cymodocea* are also present. Here and there are isolated boulders or patches of reef, and scattered colonies of *Pocillopora bulbosa* are a characteristic feature. *Stoichactis* is common.

The regions of the reef between its margin and the central flat present a bewildering labyrinth of scattered patches of dead coral or boulders with sand between, the general appearance of which is illustrated in Plate XXVI, fig. 2. Among and upon the dead coral there is a secondary growth of living coral, including a considerable number of species, but usually of a scanty nature, save in the deeper pools, where it sometimes becomes fairly flourishing, though rarely comparable with an open-water growth. The population of reef-flat organisms other than corals is considerable and interesting, resembling in many ways that of an area such as the Thalamita flat at Low Isles, and varying from place to place according to whether the particular spot is exposed or not at low water. In some of the shallow areas, where there is a strong current during the ebb, conspicuous members of the fauna are curious cup-shaped and other sponges (*Phyllospongia foliascens*, etc.) and small colonies of *Tubipora*.

A small area situated on a reef-patch in one of the deeper pools was surveyed in detail. The substratum consisted of irregular masses of dead coral, with sand between ; only the tops of the masses were uncovered at extreme tides. Corals were represented by more than 70 colonies, most of them small, and there were 85 colonies of *Xenia umbellata*. A vivid blue form of the ascidian *Diplosoma virens* was abundant. The dead coral was much overgrown by short algae, including microphytic forms, and some of these were also epiphytic. The prominent algae of larger size were *Turbinaria ornata* and *Amphiroa*

*fragilissima*. The data are summarized in the following table. This represents the population of a typical area of coral growth of a scanty type.

*Surface Population of an Area 6 feet 8 inches square on Batt Reef.*

CORALS :	ALGAE :	OTHER ANIMALS :
<i>Favia</i> . 29 colonies.	<i>Turbinaria ornata</i> . 42 stems.	<i>Xenia umbellata</i> . 85 colonies.
<i>Porites</i> . 20 ,,	<i>Amphiroa fragilissima</i> —	<i>Diplosoma virens</i> . } Abundant.
<i>Pavona</i> . >10 ,,	69 countable tufts ; con-	<i>Orbitolites complanata</i> } "
<i>Acropora</i> 5 ,,	siderable amount not	<i>Eruspongia</i> . 2 specimens
<i>Pocillopora</i> 2 ,,	countable.	<i>Aplysia</i> . 1 specimen.
<i>Galaxea</i> . 1 colony	<i>Melobesieae</i> . Abundant.	Nudibranch. . 1 ,,
<i>Goniopora</i> 1 ,,	<i>Dictyosphaeria</i> }	<i>Tridacna fossor</i> . 1 ,,
<i>Coeloria</i> . 1 ,,	<i>Caulerpa</i> }	<i>Echinometra mathaei</i> 1 ,,
<i>Symphylia</i> 1 ,,	<i>Bornetella</i> }	Sedentary polychaet 1 ,,
	<i>Halimeda</i> }	
	<i>Galaxaura</i> }	
	<i>Laurencia</i> }	
	<i>Cyanophyceae</i> }	
	Present in small	
	amounts.	

At the point visited near the south-east corner, the margin of the reef forms a smooth rocky pavement, with a very gradual slope, much overgrown by mossy algae, with scattered corals—Astraeids, creeping colonies of *Acropora decipiens*, and low massive colonies of *Pocillopora*. Behind this pavement lies a wilderness of pools and boulders, from which the transition to the central flat is gradual.

Batt Reef occupies a position at the junction of the Outer Barrier proper with the series of "inner" reefs ; but from an ecological point of view it may probably be reckoned as a member of the inner series. The general appearance of some of these large inner reefs, viewed from a height, is indicated in Plate XXV. The three here represented (Eagle Island, M Reef and L Reef) were not visited, but probably have much in common with Batt Reef.

#### V. OTHER REEFS.

The descriptions of the structure and natural history of reefs of several kinds, which have now been given, can claim no more than to furnish some idea of the variations in structure and ecology which replace one another and combine in diverse ways, over a section of the Great Barrier Reef lying between Trinity Opening and Cook's Passage. It has been indicated by Spender (1930) that this section of the great reef differs considerably from that part of it which lies south of Trinity Opening. In the northern section, where the reef has a definite edge (the Outer Barrier) descending steeply to beyond the 100-fathom line, those reefs which lie between this edge and the mainland appear to be differentiated into series ; a chain of "inner reefs" between mainland and outer barrier, separated from both by channels ; and a series of "island reefs" in the steamer-channel between the inner reefs and the shore (Text-fig. 1). We have so far aimed at a characterization of the ecology of these three kinds of reef, together with that of submerged reef-patches such as must have been antecedent to any of them. Should detailed accounts of reefs southward of Trinity Opening subsequently become available, it is possible that here different types will emerge, and that there will be a greater uniformity from one to another, or at least a less marked differentiation into series.

It is now time to make some comment upon coral reefs described in the literature of the subject but outside our own experience. We do not propose at present to make

any detailed comparison between the reefs described here and those described by others, but only to indicate one or two points of interest. The time for the full comparison is not yet. Two quotations will emphasize my meaning. First, Spender, in his paper in the *Geographical Journal*, vol. lxxvi, 1930, p. 290: "There is still a great deal of information to be obtained from the measurement and examination of the surface features of coral reefs; as more results become available comparisons perhaps more valuable than individual accounts will be possible. It seems that shallow boring, mapping, and levelling could with advantage be carried out to a considerable extent before another deep boring is made, and that a more complete knowledge of reef structures and reef processes is necessary before the world problem as expressed in such a phrase as "The Problem of Coral Reefs" can be adequately treated." Second: There are necessarily, at the present stage, many structures described in the existing accounts of coral reefs of which one can only say with Professor Sollas (*Funafuti Report*, p. 24), "I do not understand it, and forbear from speculation."

In the Queensland Barrier we are dealing with a series of reefs in which coral appears to play a greater part at the present time than it does in an atoll such as Funafuti. At the latter place the coral is fairly plentiful and varied in the lagoon (which has no exact counterpart in the Great Barrier region), but on the platform of rock forming the rim of the atoll it appears, on the whole, to be distinctly scanty, as is also the case on the uppermost part of the seaward slope. "Of coral there is less than ever, and where it does occur it is in small isolated pieces" (*Funafuti Report*, p. 130). On the Outer Barrier, by contrast, the seaward regions are rich in growing coral of great variety and bulk. Here, therefore, they must add more substance to the reef than do those of Funafuti; and although their transformation into reef rock is accomplished in both places by lichenous nullipores and similar agencies, the relative importance of the coral on the Great Barrier would appear to be greater. Another apparent contrast exists in the relatively greater importance of *Halimeda* at Funafuti than on the Great Barrier. Gardiner's description of Minikoi Atoll suggests that there the proportion of coral growth is intermediate between that of Funafuti and that of the Outer Barrier.

One of the keys which will be required before the multiple lock guarding the general problem of coral reefs can be expected to yield, will be a precise comparison of those pavements of coral rock which form the fringes of reefs where they face the surf. We possess already a number of good descriptions of these, but further data, together with a study of the conditions of organic life in these fringes, will be needed before we can feel certain of the ground. In the reefs of the Queensland Barrier described in this report the pavement occurs in two forms, but is present wherever the reef faces the waves raised by the south-east trade wind or the Pacific swell. In the case of the island reefs (Low Isles and Three Isles), where the waves experienced are not of the magnitude of Pacific breakers, and also along the southern shore of Batt Reef, the seaward fringe is a simple pavement of rock, sloping gradually into the waves, much felted by mossy algae, and supporting only a low and scattered growth of coral. On an Outer Barrier reef (reaching its best exemplification in the case of Yonge Reef) the rocky seaward part of the reef is very wide; the pavement of the reef-crest lies at some distance from the breakers, and from it the seaward slope is gradual until the point at which the breakers curl over. But the slope is complicated by the presence of the low "outer ridge" (resulting in the holding-up of water behind it to form a moat) very near the breakers.

This ridge may perhaps be regarded as a fusion of the irregular, *Melobesia*-covered coral masses of the slope, which fill up much of the moat immediately to landward of the ridge ; the fusion of such masses reaching a maximum in the ridge itself. In this case the growth of corals towards and among the breakers is very rich. All the seaward zones are veneered by living *Melobesia* at Yonge Reef, but on other similar reefs these are less conspicuous.

It appears justifiable to compare the rocky seaward pavements of the more and less sheltered reefs of the Barrier, since they are made of similar material, and occur in each case in the same relations and at similar levels ; the differences may be correlated with the variations in their exposure to waves. The "lithothamnion ridge" described by Mayor in his account of the fringing reefs at Maer Island in the most northerly region of the Great Barrier is evidently another variety of this pavement.

When we turn to true atolls it is more difficult to be sure of our ground, because here complications are involved which are not necessarily present in the Great Barrier region. At the same time it is probably fair to compare the Oceanic margin of the rocky rim of Funafuti or of Minikoi with the Oceanic margin of Yonge Reef. However different the history of these several structures may have been, the similarity may well be due to comparable combinations of conditions. There seems to be a distinct correspondence between the rocky "reef-flat" followed to seaward by a "fissure zone" ("lithothamnion zone" of Funafuti) of these atolls, and the seaward parts of Yonge Reef, where the zone centring about the outer ridge, though less fissured than the outermost zone of the atolls, may nevertheless be the equivalent of a "fissure zone."

That these pavements, as well as the rocky reef-face which descends from them, may be superficial structures, is suggested by the borings both at Funafuti and at Low Isles ; and although these reefs are so different that no far-reaching comparison between them is possible, they may, in this particular, resemble one another. This idea is expressed for Funafuti by Sollas (Funafuti Report, p. 27), when he says : "Thus too much stress must not be laid on the unconsolidated material met with in our bore-holes ; the exterior of the atoll may be faced with solid limestone, which, like a retaining wall, may hold up the looser deposits within." In the case of Low Isles such knowledge as we possess indicates that the reef-face is rocky and that the flat is underlain by mud.

Even from this brief comparison of reefs it will have been noticed that there is no uniformity of usage with regard to the nomenclature applied by different investigators to the several parts of the reefs which they describe. Thinking that uniformity of nomenclature is desirable wherever it can be attained, we studied a number of accounts of reefs with the idea that some standard set of terms might be worked out, taking as a model, for instance, the classical report on Funafuti. The variation from one to another, however, is so great that no degree of uniformity seems to be attainable. On reflection it is proper that, at the present stage of our knowledge of reefs, this should be the case. The number of different kinds of reef in existence is considerable ; and the workers on each type have developed a nomenclature which was locally suitable. An attempt to apply the same terms throughout would involve the assumption that the several features named were homologous throughout the series ; and at present we are not in a position to establish general homologies with any degree of security. The existing nomenclature offers serious difficulty only when a single term has been employed in widely different senses ; but this can only be corrected when fuller knowledge makes a definitive classification possible.

Further comments on the reefs of the Great Barrier will be found in the next section.

## SUMMARY AND CONCLUSIONS.

(By T. A. STEPHENSON.)

The following statement provides a summary of the foregoing pages, supplemented by an interpretation of the principal structural features which have been described. This aims at making it possible to view the numerous facts set out above in proper perspective, and at indicating the connection which exists between the history and structure of the reefs and the history and composition of their flora and fauna. The view of the reefs outlined here has developed from the joint ecological and geographical work of the expedition; but it makes no pretence to be anything more than a working hypothesis which correlates the facts as we know them up to the present time. Full discussions of the reefs from the geographical point of view will be found in papers recently published by J. A. Steers (1929, 1930\*) and M. A. Spender (1930).

I. SEAWARD SLOPES.—The seaward slopes of all the reefs examined by us are those places in which abundant growth of living coral is taking place. This cannot fail, even if very slowly, to add substance to the reef face; since, as the coral dies, part of it, already attached to the pre-existing dead coral of the slope, will become an integral part of that slope. This must be the case, even if the greater part of the living coral were torn up in times of storm, and were deposited, some of it farther down the seaward slope and some of it on the edge of the reef. On the basis of this argument the assumption which has often been made, that the reef grows slowly outward (it cannot grow upward once it has reached the surface), appears to be perfectly reasonable.

II. ROCKY PAVEMENTS.—We have described rocky pavements or platforms of several kinds in connection with several reefs. Some of these appear to form a series. It has been argued (p. 91) that the seaward parts of Yonge Reef, the windward pavement of Batt Reef, and the windward shelf of Low Isles, are probably homologous structures. In the light of this the true importance of the windward shelf at Low Isles, at first sight so inconspicuous, becomes apparent; it is to all appearance the normal rocky reef-margin of the surf-zone; but attention is distracted from it by the more obvious structures, the ramparts, mangrove swamp and cay.

III. REEF FLATS.—We have no knowledge of the actual conditions which induce the formation of sandy reef-flats; but such flats may reasonably be regarded as accumulations of sediment which appear during certain phases of the development of reefs subject to given conditions. At Low Isles there is the complication that part of the reef-flat is rocky, consisting of the honeycomb-rock described on p. 52 and illustrated in Text-fig. 8. The explanation of the presence of this is not clear. Flat slabs of coral rock can and do arise *in situ* on reef-flats (Plate VIII, fig. 4; Plate IV, fig. 1), by the gradual lateral extension, in shallow water, of colonies of corals, such as *Porites*, which die on the top, but remain living for some time round the edges. By the fusion of such masses fairly extensive platforms may be formed, and this probably explains the origin of the rocky area in the western and middle moats, mentioned on p. 49. On the other hand, the main tract of honeycomb-rock of the Low Isles flat is so extensive and of so suggestive a shape that it seems possible that it is due to another cause. Whether it represents some earlier position of a marginal pavement, or a vestige of some other former state of the reef, is a question

\* Steers' 1930 paper is report No. 1 in this volume.

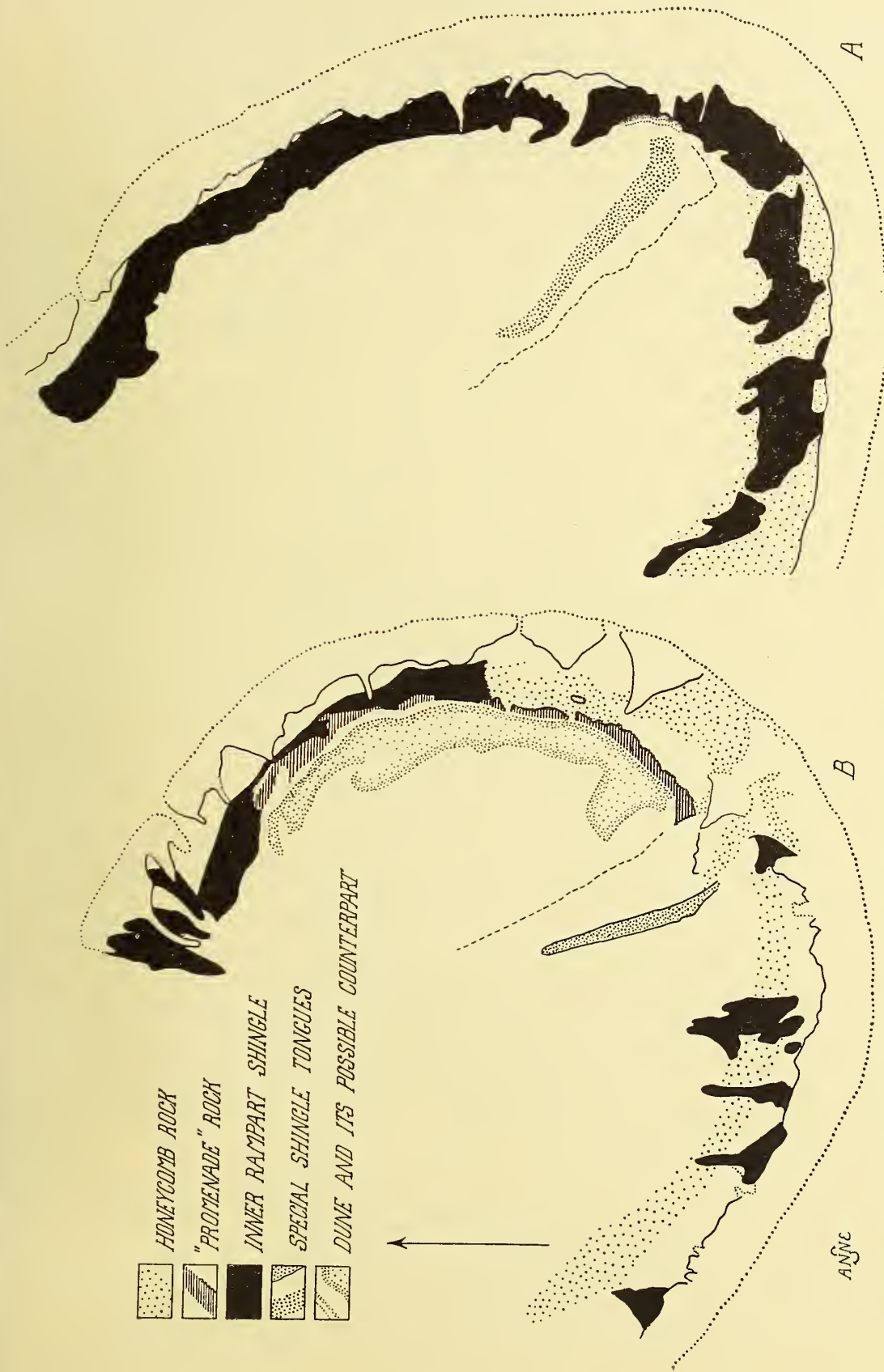
for the decision of which we have so far insufficient data ; the possible explanations which we have proposed to ourselves are open to too many objections to enable us to present any one of them with confidence. On the other hand, it may be noted that there are several agencies at work on the reef, both at and beneath the surface, which may tend towards the disintegration of coral rock on the flat. These agencies include, apart from the ordinary activities of boring organisms, bacterial liberation of CO<sub>2</sub> during disintegration of organic material contained in the rock itself (derived from boring and crevice-living forms), in the sand associated with it, and in the mangrove mud (see p. 70).

IV. DISPOSAL OF DEBRIS.—It may be argued that the fate of reef-debris will depend upon local conditions—upon the angle of the seaward slopes ; the level of the top of the reef ; the strength of the waves to which the reef is exposed ; the depth to which their destructive action is effective in stormy weather ; the nature of the coral growth upon the slope ; and the level at which the maximum growth of coral occurs. If this be the case the disposition of debris will vary not only on different reefs, but in different parts of the same reef, according to the exact combination of the factors concerned, at any particular spot. On a reef such as Yonge Reef there is no significant amount of debris on the oceanic side until the boulder zone is reached ; but there is, doubtless, an accumulation of it down the steep seaward slope. At Low Isles there is a great accumulation of surface debris, much of it of a comparatively fine grade, round the windward arc (ramparts), and on the seaward slope at the south-east corner there is the curious double profile, gradual at first, then steeper, and afterwards more gradual again, described on p. 64. These changes of angle possibly indicate the situation of debris which has descended the slope. On the leeward side there is the boulder tract, where large surface-debris reaches its maximum ; and this is probably to be explained as the result of the action of occasional hurricanes blowing from a direction opposite to that of the prevailing wind and tearing up large masses of coral which have become unusually unwieldy or unstable, growing into exaggerated shapes, as a result of the sheltered conditions under which they usually live.

V. RAMPARTS, MANGROVE SWAMPS AND CAYS.—Here I wish to make three points. First : That the “ island reefs ” in the steamer channel off the Queensland coast north of Trinity Opening (Class V reefs of Spender) are *coral reefs* upon which ramparts and mangrove swamps have been formed as superficial structures. The reefs upon which these structures lie have their flats at an unusually high level\* (probably as the result of a slight degree of emergence which they share with the mainland), and are anomalous also in the fact that their flats, if we may judge from the borings at Low Isles, are underlain by soft mud. But the reef proper, without its superficial additions, may be regarded in the present state of our knowledge as consisting of the windward pavement and seaward slope, with their reef-flat ; and in this sense resembles an “ inner reef ” such as Batt Reef, and is, from a biological point of view, of an ordinary kind. Cays, as opposed to ramparts, can and do appear on reefs which we believe to be of lower level than those of Class V ; on a reef of the latter class the cay will antedate the rampart.

Second : The conditions which are responsible for the formation of these cays, ramparts and swamps (discussed fully by Spender, 1930), appear to be connected with the size, shape, level, orientation and situation of the reef, which factors may be held to

\* The level of the flat has been ascertained by measurement only in the case of Low Isles ; but “ so far as is known this is also in agreement with the flats of the other reefs of this type.” (Spender, 1930, p. 285.)



TEXT-FIG. 15.—An attempt to compare the inner rampart of Low Isles (represented in solid black in fig. A), with the region which occupies a corresponding position at Three Isles. The areas of shingle at Three Isles which are most similar to inner rampart material at Low Isles are represented in black, and the narrow bank of shingle at Low Isles which possibly corresponds to the Three Isles dune is indicated in the same convention as the dune. For further details see p. 96. The two very long shingle-tongues shown probably do not correspond exactly—the one in fig. A lies *inside* the border of the mangrove area and probably has an exact counterpart at Three Isles (as yet unsurveyed). Similarly, the long tongue of Three Isles, which lies *outside* the border of the mangrove area, may correspond to an ill-defined ridge which occupies an almost exactly similar position in the mangrove park at Low Isles.

determine the degree and incidence of the wave action to which it is exposed. On this interpretation cays will be products of one combination of conditions, ramparts of another, but mangrove swamps are apparently a development which, under suitable circumstances, will follow the formation of ramparts. A rampart having been formed, mangrove seedlings can establish themselves on its inner scarp and on the flat in its shelter \* ; in time they will spread, and creating their own mud from the decay of mangrove material, they will form a swamp on the top of the sand of the flat.

Third : That ramparts appear to be able to encroach for a certain distance only over the reef-flat† and that one wave of shingle follows in due course upon another. This suggests that rampart systems probably undergo a cyclic type of development after their inception, so that the exact state of affairs on any one reef will represent a phase in the cycle. Thus the inner rampart at Low Isles is compacted and partly transformed into conglomerate and is also considerably eroded ; the outer rampart is encroaching upon it and is loose and comparatively recent. At Three Isles (Text-fig. 15), there is no inner rampart proper, though a region of shingle very like one exists for a short distance ; but the area between dune and outer rampart presents a complex structure and includes the promenades of hard rock described on p. 30. These two regions correspond both in shape, width, height, and relations on the two reefs ; and we interpret this correspondence as meaning that the promenades at Three Isles may be the remains of a former rampart which has undergone not only a further transformation into rock than the inner rampart at Low Isles, but also a greater degree of erosion, so that the softer parts have been extensively dissected away. The honeycomb rock which figures in this area at Three Isles has the appearance of forming part of the windward platform of the reef, but it is conceivable that even this represents, in part, the planed-down vestige of former ramparts. The dune of Three Isles appears to be a structure comparable to a narrow bank of loose shingle‡ which is present along part of the inner edge of the inner rampart at Low Isles ; but the dune has reached a much more highly developed condition, and has attained a size and height which enable it to support dry land vegetation.

VI. To my mind it has emerged clearly from the work of the expedition that it is at present improper to speak of " a typical coral reef," and that, if such a thing exists, it cannot yet be defined. It might be argued that the phrase " a typical coral reef " could be used in two senses—on the one hand as referring to reef-structure, and on the other as expressing the biological point of view ; but in either case a deeper knowledge is needed both of the foundations of reefs, and of the biological processes which take place on them, before we can make any statement as to what, if anything, is typical. This affects the question of Low Isles in the following sense : with the reservations just made, and from the biological point of view, Low Isles may be regarded as a reef which (apart from its distinction in bearing ramparts, etc.) is as near to being a " typical " reef as many another. It must at least be defined as a coral reef.

\* See Plate IV, figs. 2-4 ; Plate XI, fig. 2 ; Plate XII, fig. 4 ; Plate XIII, fig. 4.

† This must of course be taken as applying to reefs subject to conditions similar to those which obtain at Low Isles. Measurements of the distances which the shingle of the inner rampart has actually traversed at Low Isles, and of comparable distances at Three Isles, suggest that the limiting distance for the travel of shingle is of the order of 700 ft. from the low-water margin of the reef ; it is perhaps a little greater for Three Isles than for Low Isles, because of the greater violence of the wind at the former place. The very long tongues do not appear to belong to the same system and are not included in this reckoning.

‡ This bank is shown in Plate XXVII and in Text-fig. 15, and part of it in Plate XIII, fig. 2.



VII. The content of the last paragraph may appear self-evident to anyone who has read this report ; but it has not always been realized. It has been frequently suggested verbally, and at least once in print, that Low Isles is "not a typical coral reef," from which the conclusion is sometimes drawn that it does not illustrate favourably the problems of reef formation and reef biology in general. This idea is erroneous ; the coral growth at Low Isles is, in fact, thoroughly varied and luxuriant ; but it must be sought in the proper places. Elsewhere in the Great Barrier region it is, perhaps, surpassed, as for instance in parts of Yonge Reef, but by little. Several of Saville Kent's well-known photographs of rich coral growths might easily have been secured at Low Isles, and were actually taken on a similar island reef. It must be remembered that many of Kent's photographs represent coral-associations belonging to comparatively low levels, and exposed only at extreme tides—growths which were chosen for their attractive quality from the point of view of a photographer. It is possible to walk for miles along many a reef of the Great Barrier without seeing anything of the sort, and so long as the proper zones were not sought out, a "Saville Kent" picture might never be seen at all.

VIII. THE SHAPES OF REEFS.—Low Isles is a reef of curious shape. The logical outlines for reef-systems of this type, which might be expected to result from the moulding effect of the forces to which they are exposed, include that of Three Isles (a simple ovate) and also horse-shoe forms. Low Isles presents, however, the curious embayment in its south-west coast which distorts it from a simple shape. This is perhaps due to a double foundation : Low Isles may be founded not upon one reef, but upon two or more, lying close to one another, which grew together or became united by infilling of sediment at a certain phase in their history. Several features suggest this, among them the existence of the south-west shelf (this would be the small windward shelf of the smaller and more sheltered of the two reefs) and the difference of level between the eastern and western parts of the flat.\* This leads on to the observation which should be kept in mind during the future study of such reefs, that the exact form of a mangrove, rampart and cay-bearing system may be expected to depend first upon the size, shape, number and relative positions of the reef patches upon which it is founded, and upon the depths from which they grow, and later upon the effects of currents and of the waves created by the prevailing south-east wind (Text-fig. 3) ; but this second influence cannot always obliterate the effects of the first.

IX. The history of Low Isles must, therefore, be somewhat as follows. Reef patches of the type described on p. 88 at first grew up from the sea floor, bearing living coral on the top as well as down the sides. On reaching the surface the coral on top was killed, leaving only the seaward slopes to add to the substance of the reef. A windward pavement and a reef flat were formed in connection with the reaching of surface level. During the later stages first a cay and subsequently a rampart were developed, and after this a mangrove swamp. This outline, whilst omitting much, gives enough to make possible an analysis of the flora and fauna.

X. The fauna and flora of Low Isles, therefore, include the following elements :

1. The rich and varied growth of corals and alcyonaria which is proper to submerged reef patches (*cf.* the one described at Lizard Island, p. 88), but which at Low Isles has

\* The general level of the eastern part of the flat is about 4 ft. above datum, this region being bounded approximately to westward by a curve running from Tripneustes Spit to M1. The western flat (*i. e.* the Sand flat and Thalamita flat) lies about  $2\frac{1}{2}$ –3 ft. above datum.

survived only on the seaward slopes and in the anchorage. Associated with this growth are other organisms of various kinds, amongst which clams and fishes are conspicuous.

2. A purely secondary growth of coral, of a limited number of species, which has been able to establish itself in the pools of the flat, especially the moats; together with associated organisms.

3. A series of plants and animals which are able to stand the conditions of a tidal flat. Apart from those which bury themselves in the sand, and which are, therefore, segregated, these organisms tend to be ubiquitous on the flat; but since the flat varies in nature from place to place in a number of ways (nature of substratum, depth of pools available at low water, vicinity of mangroves, etc.), so does the fauna and flora vary subtly in composition, certain species tending to congregate most distinctly in regions where particular combinations of these conditions occur.

4. The presence of the ramparts provides a habitat found only on reefs of certain kinds, and situated at a fairly high level; with it are associated a fauna and flora of in-crusting or crevice-living forms which draw their population not only from the reef-flat series of species, but also from that of the mangrove area. It is also a special feature of the ramparts that certain animals which, on a mainland shore or on a reef with no rampart, would perforce occupy different habitats, choose the ramparts as a particular headquarters. The inner rampart is intermediate between the mangrove area and the outer rampart in population as in position.

5. The presence of the mangrove swamp introduces a new element into the fauna and flora. In the first place it carries with it a population of forms which would normally have no connection with the fauna of a reef. Secondly, it provides migrant species which escape beyond it and affect the fauna of ramparts and mangrove park. Thirdly, it provides curious areas, the mangrove park and parts of the swamp itself, in which reef conditions and woodland conditions are mixed, and in which, although a number of the reef organisms are able to flourish, the nature of the fauna and flora is recognizably modified. Certain organisms such as the hydroid *Myrionema amboinense* and the alga *Caulerpa verticillata* seem to be particularly at home under these peculiar conditions.

6. In addition to the graded series of regions just enumerated, in which the original fauna of the reef and the introduced fauna can to some extent mingle, there is dry land, which supports associations of its own sharply different from those of the rest of the reef. Dry land organisms and mangrove organisms meet in the swamp, but between those of the dry land and those of the reef there is little contact.

7. The zonation of life according to level, therefore, follows broadly the regions already indicated: from above downwards, dry land; beach sandstone and ramparts; flat and mangrove swamp; seaward slope and anchorage. On the sandstone and ramparts, however, there is further zonation from the higher to the lower parts, and the same applies to the seaward slope and anchorage, on which coral species in particular exhibit a distinct zonation. On the flat zonation is less apparent, since the factors which regulate distribution there (see paragraph 3) differentiate the region horizontally more than vertically; but even here it is the variations in level which determine the depth and extent of the pools available at low water; and they may be effective in other ways.

8. The fauna and flora of the other reefs which have been described may be understood in their relation to those of Low Isles with little further comment. Three Isles offers an almost exact parallel to Low Isles. Some of the reef-patches off Lizard Island

provide a picture of the population of reefs which are submerged or occasionally slightly exposed at low water of springs, and which possess no reef-flat. Yonge Reef has a flora and fauna of a similar nature, in which corals, aleyonaria, clams and Melobesieae are conspicuous; it is essentially the population of a submerged reef adapted to the immediate vicinity of the Pacific, but one which partly uncovers a limited number of times in the year. Batt Reef is a case in which the principal development of this typical population is restricted to the fringes, the advent of a vast sandy flat having introduced modifications of a new type, with correlated faunal and floral changes. Low Isles and Three Isles represent a still greater modification from the conditions of a submerged reef-patch. In all these cases the general level of the top of the reef is an important factor in determining the conditions which affect organisms.

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## A COMMENT ON THE INSTRUMENTAL SURVEY.

(By M. A. SPENDER.)

The need for a second geographical comment in these reports is not immediately apparent. The second geographer's work was survey. Nevertheless, the fact that the maps and sections resulting therefrom are published here, calls for some explanation. These detailed surveys of two reef systems were made in close collaboration with the biological side of the expedition; the interdependence of the two aspects of reef work was apparent to us in the field, and indeed it is apparent in these published reports. Some discussion of the surveys from a geographical point of view has been published elsewhere (*Geographical Journal*, vol. lxxvi, 1930, pp. 193 and 273); but the maps and sections are published here out of the necessity of the biologists. It is fair to say that hitherto the workers on coral reefs have had to manage as best they could on pre-existing maps of small scale. Although at Funafuti they had a special survey, they were handicapped in the same way in describing the detail of the reef's surface; for charts are constructed to assist mariners in steering with safety amongst reefs. Structure of the reef itself is outside the hydrographer's scope.

That there was no precedent to guide our work gave us some difficulty in the conventional representation of an amphibious region. It was necessary to evolve a set of symbols that were as far as possible self-expressive, and that could modify one into another according to the changes in the reef surface. Those embodied in this report were worked out by collaboration between the biological and the geographical parties, and are not the least important part of the work.

To my mind the most weighty constituent of our joint work was that connected with levels. On the results of this expedition, we are able to state, with a high degree of accuracy, that such a part of the reef or such a zone of corals is found at a level so many feet above or below datum or mean sea-level. The value of the accurate relation, where estimation can be so misleading, of organisms to tide levels is readily appreciated. The figures, so easily expressed, were not always simply obtained; in particular this work depends on the erection of a tide-gauge. A tide-gauge is expensive, cumbersome to transport, difficult to erect and an anxiety to maintain in running order. But without proper

reference to extreme tides and mean sea-level, the detailed biological traverses described in a subsequent paper would lose much of their value. This quantitative work will only fully assert itself when other work is available with which the Low Isles work can be compared.

It is true that if a geographer could achieve no more than a faithful record of the island reef as he saw it, his science would be amply served. If that first party of investigators, Captain Owen Stanley, J. Macgillivray and T. H. Huxley, who landed on Low Isles eighty years ago, had been able only to make it indubitably clear how many islets lay on the reef, we who followed them would have been grateful. Had the position in which they lay been charted, the whole course of the geographical work and conclusions might have been different. That of which we are sure may seem shamefully scanty to us, but on its sureness will its value to anyone else depend.

## DESCRIPTION OF THE SURVEY.

### LOW ISLES.

A base line was measured with a steel tape on the high eastern part of the flat; no elaborate precautions were taken. This was extended to the beacon stations (marked  $\Delta$ ), whose positions were fully triangulated. Tacheometric traverses were run with the theodolite between these stations outside the mangroves and along some parts of the rampart. The rest of the detail was plotted in with the plane table, except for the inside of the mangrove swamp, where the photographs made by 101 Flight of the R.A.A.F. were adjusted to show the open glades.

The soundings were made with a hand lead-line from an open boat, positions being plotted with the sextant and station pointer, and adjustments for depth taken from the recording tide-gauge.

The levelling was done with a Watts-Zeiss reversible level, most of the traverses being closed. The permissible error was 0.03 ft. per mile, such errors as occurred being due to the difficulty of finding a secure foundation for the staff.

The triangulation points were marked with stakes of stainless steel specially supplied by Messrs. Firth of Sheffield. These stakes were very convenient for this purpose and and for every other occasion where a position and level had to be left in the reef for the course of the work.

Throughout the survey, difficulty was experienced on account of the distortion of the paper in the climate.

### THREE ISLES.

This was a quick survey. The base-line was measured on the flat tacheometrically while the flat was still covered by the tide. The beacon stations were intersected from the extended base-line.

A compass and tape traverse was run outside the mangroves. The remainder of the detail was filled in with the plane-table and paced compass traverses between previously fixed points. No levelling or sounding was attempted.

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## APPENDIX.

The types of rock mentioned in this paper come under the following headings.

A. BEACH SANDSTONE.—A rock composed of sand derived from the skeletal remains of coral and other organisms. The grains are cemented together by calcium carbonate deposited between them. This rock occurs only round the slopes of sand cays, on the reefs here described.

B. SHINGLE CONGLOMERATE.—A rock formed from coral shingle, which, on the reefs described, occurs only in connection with shingle ramparts or with regions which may represent the remains of such. It is not found among the part of the shingle which appears to be the most recent.

C. CORAL ROCK.—This phrase is employed in the present paper as a general term covering both boulders made of dead coral and more continuous masses or pavements which are also made of dead coral. It includes besides these the “promenades” of Three Isles, which, although described simply as “coral rock,” may be thought of as a derivative of shingle conglomerate.

D. HONEYCOMB-ROCK.—This is a special case of “coral rock,” and is defined on p. 52.

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## REFERENCES.

It seems needless to give here an extensive bibliography of works relating to coral reefs, since one has recently been published by W. M. Davis ('The Coral Reef Problem,' American Geographical Society, special publication No. 9, New York, 1928, p. 549). We therefore give a brief analysis of such of the literature as has proved most interesting and useful to us in the preparation of this report, with the aim of providing an introduction to the whole literature of the subject. Further references may be obtained from the works quoted.

1. *The Coral Reef Problem in General.*

- DARWIN, CHARLES. 1842. On the Structure and Distribution of Coral Reefs, pp. xii + 214, 3 maps, text illust. London.
- DAVIS, W. M. 1928. The Coral Reef Problem. American Geographical Society, special publication No. 9. New York. Pp. v, 596, 15 pls., text illust.
- GARDINER, J. STANLEY. 1915. Submarine Slopes. Geogr. J. XLV, pp. 202-219, 2 pls., text illust.

2. *The Australian Barrier Reef.*—A valuable account of the Barrier Reef will be found in the work of Jukes; very fine photographs in that by Saville Kent; a useful summary of the literature in the paper by Steers; the most recent discussion of the reefs in that of Spender; and various information in the two volumes of reports of the Great Barrier Reef Committee.

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*Vol. I contains the following papers in the order here given:*

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- HEDLEY, C. The Natural Destruction of a Coral Reef, p. 35.
- HOGAN, J. Record of Sea Temperatures observed at Willis Island during the Cyclone Season of 1922-1923, p. 41.
- ALEXANDER, W. B. Sea-birds of the Great Barrier Reef, p. 47.
- PARADICE, W. E. J. The Pinnacle or Mushroom-shaped Coral Growths in Connection with the Reefs of the Outer Barrier, p. 52.
- HEDLEY, C. A Raised Beach at the North Barnard Islands, p. 61.
- The Townsville Plain, p. 63.
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- A Disused River-mouth at Cairns, p. 69.
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- The Drainage of the Atherton Tableland, p. 131.
- HEDLEY, C. The Surface Temperature of Moreton Bay, p. 149.
- The Queensland Earthquake of 1918, p. 151.

*Vol. II contains the following:*

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- STANLEY, G. A. V. The Physiography of the Bowen District, etc., p. 1.
- EDGEHILL, J. A. Some Remarks on Coral Formations, p. 52.
- Changes at Mast Head Island, p. 57.
- BRYAN, W. H. The Queensland Continental Shelf, p. 58.

- JARDINE, F. The Topography of the Townsville Littoral, p. 70.  
 — The Broadsound Drainage in Relation to the Fitzroy River, p. 88.  
 — Bramble Cay, Torres Strait—Geological Notes, p. 93.  
 — Darnley Island—Geological and Topographical Notes, p. 101.  
 PARADICE, W. E. J. The Divergence of the Ends of the Great Barrier Reef from the Coast, p. 110.

*The Committee has also issued the following booklet :*

The Great Barrier Reef of Australia. A popular account of its general nature, compiled by the Great Barrier Reef Committee, Brisbane, 1926. Queensland Govt. Intelligence and Tourist Bureau, Brisbane. 32-page pamphlet. A new edition of this has been issued since the termination of the Expedition.

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3. *References to Low Isles.*—These will be found in the following works. Some short articles on the fauna of Low Isles, written by members of the staff of the Australian Museum after visiting the Barrier Reef Expedition, will be found in the Australian Museum Magazine, vol. iii, 1928-9, pp. 313, 330, 366. The results of the Geographical section of the Expedition are published in the papers listed under section 2 of this list, by Steers and Spender.

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*Vol. V :*

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## SYSTEMATIC INDEX.

## ANIMALS.

PROTOZOA.		PAGE	COELENTERATA—cont.	
Ciliates . . . . .		70	ANTHOZOA.	PAGE
Flagellates . . . . .		70	Anthozoa . . . . .	56, 71
Foraminifera . . . . .		44, 70	(1) <i>ALCYONARIA</i> .	
Orbitolites complanata . . . . .	44, 48, 50, 70, 90		Alcyonaria . . . . .	49, 61, 64-67, 70-72, 83, 84, 86-88, 97, 99
Protozoa . . . . .		70	Alcyonium . . . . .	67
			Cespitularia multipinnata . . . . .	67, 82
PORIFERA.			Clavularia . . . . .	67
Chalina camerata . . . . .		38, 54	Dendronephthya . . . . .	67
,, clathrata . . . . .		38, 54	Gorgonians . . . . .	71
Chondrilla nucula . . . . .		54	Heliopora . . . . .	50, 67, 71, 72, 81, 86
Cinachyra australiensis . . . . .	44, 52, 53		Heteroxenia . . . . .	67
Cladochalina pulvinatus . . . . .		38	Isis hippuris . . . . .	82, 88
Clathria aculeata . . . . .		44	Juncella . . . . .	67, 71
Desmacidon reptans . . . . .		54	Lithophytum . . . . .	67
Euspongia . . . . .		90	,, arboreum . . . . .	86
,, irregularis var. pertusa . . . . .	44, 52, 71		,, digitatum . . . . .	86
Gellius fibulatus . . . . .	44, 48, 49, 54		Lobophytum . . . . .	67, 86, 87, 88
,, pumilus . . . . .		38	Melitodes . . . . .	67, 71
,, sagittarius . . . . .	44, 48		Pachyclavularia . . . . .	67
,, toxius . . . . .	38, 39		Sarcophytum . . . . .	64, 67, 86-88
Iotrochota purpurea . . . . .		54	Sinularia . . . . .	64, 67, 86-88
Laxosuberites proteus . . . . .		54	,, flexibile . . . . .	87, 88
Ophlitaspongia rimosa . . . . .		54	Tubipora . . . . .	71, 84, 86, 89
Phyllospongia foliascens . . . . .	71, 86, 89		Xenia . . . . .	67, 86
,, ridleyi . . . . .	83, 84, 86		,, umbellata . . . . .	89, 90
Polymastia . . . . .		54	(ii) <i>CERIANTHARIA</i> .	
Porifera . . . . .	44, 54, 86		Arachnanthus . . . . .	56, 72
Pseudosuberites andrewsi . . . . .		54	(iii) <i>ANTIPATHARIA</i> .	
Rhaphidophilus coralliophilus . . . . .		54	Eucirripathes . . . . .	67, 72
Spirastrella aurivillii . . . . .		54	(iv) <i>ZOANTHINARIA</i> .	
,, purpurea . . . . .	38, 44, 52, 71		Palythoa . . . . .	65, 67, 72, 84, 86, 88
,, semilunaris . . . . .		54	Zoanthids . . . . .	38, 49, 52, 84
Spongelia digitata . . . . .		38	Zoanthinaria . . . . .	44, 67, 72, 86, 88
Sponges . . . . .	38, 39, 42, 54, 70, 71, 83, 84		(v) <i>ACTINIARIA</i> .	
Stelletta purpurea . . . . .		86	Actiniaria . . . . .	44, 72
			Actinodendron plumosum . . . . .	44, 47, 50, 54, 55
COELENTERATA.			Anemones . . . . .	36, 42, 47, 58
Coelenterata . . . . .		38, 54, 59, 71	Anemonia citrina . . . . .	57
HYDROZOA.			Anthopleura . . . . .	36, 59
Aglaophenia cupressina . . . . .	71, 83, 84, 86, 88		Calliactis miriam . . . . .	72
Dynamena crisioides . . . . .	44, 54, 59, 71		Commensals . . . . .	47, 72, 73
Hydroids . . . . .		42	Cryptodendron adhaesivum . . . . .	47
Hydrozoa . . . . .	44, 67, 71, 86, 88		Edwardsia . . . . .	56
Lytocarpus phoenicius . . . . .		67	Gyrostoma ramsayi . . . . .	72, 87
Millepora . . . . .	38, 67, 71, 86		Phellia . . . . .	59
Myrionema amboinense . . . . .	38, 44, 49, 52, 71, 98		Phyllo-discus cinctus . . . . .	38
Sertularia . . . . .		84, 86	Phymanthus . . . . .	54, 56
			Stoichactis . . . . .	73, 89
SCYPHOZOA.				
Cassiopea andromeda . . . . .		50, 71		

COELENTERATA—*cont.*

ANTHOZOA— <i>cont.</i>	PAGE
(v) <i>ACTINIARIA</i> — <i>cont.</i>	
<i>Stoichactis kenti</i> . . . . .	38, 44, 47, 49, 50, 54, 72
<i>Thalassianthus</i> . . . . .	73
„ <i>hemprichii</i> . . . . .	47
„ <i>hypnoides</i> . . . . .	47
(vi) <i>MADREPORARIA</i> .	
<i>Acanthastrea</i> . . . . .	47
<i>Acropora</i> . . . . .	38, 57, 62, 67, 82-86, 88, 89, 90
„ <i>brueggemanni</i> . . . . .	82
„ <i>decipiens</i> . . . . .	83, 90
„ <i>delicatula</i> . . . . .	83
„ <i>gemmifera</i> . . . . .	83, 84
„ <i>hebes</i> . . . . .	44, 46, 47, 62, 82, 84
„ <i>hyacinthus</i> . . . . .	83
„ <i>palifera</i> . . . . .	83, 85, 88
„ <i>pulchra</i> . . . . .	62, 82, 84
„ <i>squamosa</i> . . . . .	84
<i>Actinotryx</i> . . . . .	47
<i>Astraeids</i> . . . . .	38, 90
<i>Astreopora</i> . . . . .	67, 86
<i>Coclوريا</i> . . . . .	67, 86, 88, 90
<i>Commensals</i> . . . . .	47, 66, 73
<i>Corals</i> . . . . .	26, 28, 34, 37, 42, 47, 49, 50, 53, 57, 60-62, 64-66, 70, 72, 73, 83-85, 87-99
<i>Cyphastrea</i> . . . . .	39, 50, 54, 67, 86
<i>Dendrophyllia</i> . . . . .	67
<i>Diploastrea</i> . . . . .	67
„ <i>heliopora</i> . . . . .	88
<i>Discosomidac</i> . . . . .	88
<i>Echinopora</i> . . . . .	67, 86, 87
<i>Euphyllia</i> . . . . .	67, 73, 86
<i>Favia</i> . . . . .	41, 47, 54, 67, 71, 74, 80, 84, 86, 88, 90
<i>Favites</i> . . . . .	47
<i>Fungia</i> . . . . .	49, 67, 73, 88
<i>Galaxca</i> . . . . .	44, 67, 86, 87, 90
<i>Goniastrea</i> . . . . .	47
<i>Goniopora</i> . . . . .	67, 86, 89, 90
<i>Herpetolitha</i> . . . . .	67, 88
<i>Hydnophora</i> . . . . .	67, 86
<i>Leptastrea</i> . . . . .	39, 44, 50, 67
<i>Lobophyllia</i> . . . . .	67, 86, 88
<i>Madreporaria</i> . . . . .	44, 67, 72, 86, 88
<i>Merulina</i> . . . . .	67, 88
<i>Montipora</i> . . . . .	38, 64, 67, 86, 88
„ <i>ramosa</i> . . . . .	44, 46, 47, 62, 82
<i>Orbicella</i> . . . . .	67
<i>Oulophyllia</i> . . . . .	67, 87
<i>Pachyseris</i> . . . . .	67, 87
<i>Pavona</i> . . . . .	67, 81, 86, 87, 90
<i>Platygyra</i> . . . . .	67, 86, 88
<i>Pocillopora</i> . . . . .	67, 86, 88, 90
„ <i>bulbosa</i> . . . . .	38, 44, 47, 50, 89
<i>Polyphyllia</i> . . . . .	67, 88

COELENTERATA—*cont.*

ANTHOZOA— <i>cont.</i>	PAGE
(vi) <i>MADREPORARIA</i> — <i>cont.</i>	
<i>Porites</i> . . . . .	38, 39, 44, 46-48, 50, 54, 67, 72, 80, 82, 86, 87, 89, 90, 93
<i>Psammocora</i> . . . . .	49, 67, 87
<i>Rhodactis</i> . . . . .	47
<i>Seriopora</i> . . . . .	67, 86, 88
<i>Stylophora</i> . . . . .	67, 86, 88
<i>Symphyllia</i> . . . . .	67, 74, 80, 86, 88, 90
<i>Tridacophyllia</i> . . . . .	67, 87
<i>Turbinaria</i> . . . . .	67, 88
<b>CTENOPHORA.</b>	
<i>Coeloplana</i> . . . . .	72
<b>TURBELLARIA.</b>	
<i>Turbellaria</i> . . . . .	72
<b>NEMERTINEA.</b>	
<i>Baseodiscus</i> . . . . .	56
„ <i>delineatus</i> . . . . .	72
„ <i>quincelincatus</i> . . . . .	56, 72
<i>Lineus</i> . . . . .	56, 72
<b>ANNULATA.</b>	
<b>POLYCHAETA.</b>	
<i>Eurythoe complanata</i> . . . . .	44, 56, 72
<i>Galeolaria caespitosa</i> . . . . .	70
<i>Iphione muricata</i> . . . . .	44, 54, 72
<i>Marphysa mossambica</i> . . . . .	56
<i>Mesochaetopterus minuta</i> . . . . .	56
<i>Odontosyllis hyalina</i> . . . . .	73
<i>Perinereis obfuscata</i> . . . . .	72, 73
<i>Phyllodoce malmgreni</i> . . . . .	56
<i>Platynereis polyscalma</i> . . . . .	72
<i>Polychacta</i> . . . . .	38, 44, 54, 56, 67, 72, 86, 90
<i>Scolelepis indica</i> . . . . .	56
<i>Spirobranchus</i> . . . . .	85
„ <i>giganteus</i> . . . . .	44, 48, 67, 72, 83, 86
Worms . . . . .	55
<b>OLIGOCHAETA.</b>	
<i>Earthworms</i> . . . . .	40, 41
<i>Pontodrilus bermudensis</i> . . . . .	40, 42, 73
<b>GEPHYREA.</b>	
<i>Aspidosiphon cumingii</i> . . . . .	56, 59, 60
<i>Cloeosiphon</i> . . . . .	59, 60
<i>Gephyrea</i> . . . . .	56, 60, 73
<i>Physcosoma</i> . . . . .	59, 60
<i>Sipunculoidea</i> . . . . .	37, 44, 59, 60, 73
<b>ARTHROPODA.</b>	
<b>CRUSTACEA.</b>	
<i>Crustacea</i> . . . . .	47, 56, 67, 70, 73
<b>(i) CIRRIPIEDIA.</b>	
<i>Acorn barnacles</i> . . . . .	37, 44, 54, 59, 70, 73
<i>Cirripectia</i> . . . . .	44, 59, 73
<i>Lepas anatifera</i> . . . . .	73

## ARTHROPODA—cont.

CRUSTACEA—cont.	PAGE
(i) <i>CIRRIPEDIA</i> —cont.	
Lithotrya . . . . .	73
Ship's barnacles . . . . .	73
Tetraclita . . . . .	73
(ii) <i>ISOPODA</i> .	
Cymodoce . . . . .	73
Isopoda . . . . .	40-42, 57-59, 61-73
Ligia australiensis . . . . .	40, 42, 59, 61, 73
(iii) <i>AMPHIPODA</i> .	
Amphipoda . . . . .	59, 73
Ampithoe . . . . .	73
Ceradocus . . . . .	73
Hyale . . . . .	59, 73
Maera . . . . .	73
(iv) <i>DECAPODA</i> .	
Decapoda . . . . .	56, 73
A. <i>NATANTIA</i> .	
Crangon strenuus . . . . .	44, 73
" ventrosus . . . . .	44, 73
Commensals . . . . .	47, 72, 73
Natantia . . . . .	44, 73
Periclimenes . . . . .	47
" brevicarpalis . . . . .	47, 73
" spiniferus . . . . .	47
Prawns . . . . .	38, 47, 70, 73
B. <i>REPTANTIA</i> .	
(a) <i>PALINURA</i> .	
Panulirus versicolor . . . . .	67, 73
(b) <i>ANOMURA</i> .	
Anomura . . . . .	42, 44, 59, 61, 73
Callianassa australiensis . . . . .	56
Callianidea . . . . .	56
Clibanarius . . . . .	73
" striolatus . . . . .	38, 40-42, 52
" virescens . . . . .	37, 44, 59, 61
Commensals . . . . .	72
Dardanus megistos . . . . .	44
Hermit crabs . . . . .	38, 39, 58, 72, 73, 83, 84
Petrolisthes lamarcki . . . . .	59, 61, 73
Thalassina . . . . .	41
" anomala . . . . .	40, 42
(c) <i>BRACHYURA</i> .	
Actaea hirsutimana . . . . .	44
" polyacantha . . . . .	47
" tomentosa . . . . .	59, 86
Atergatis ocyroe . . . . .	44, 47, 54, 59
Brachyura . . . . .	42, 44, 54, 59, 61, 74, 86
Calappa hepatica . . . . .	44, 52
Charybdis orientalis . . . . .	86
Chlorodopsis melanochirus . . . . .	59
Commensals . . . . .	47

## ARTHROPODA—cont.

CRUSTACEA—cont.	PAGE
(iv) <i>DECAPODA</i> —cont.	
B. <i>REPTANTIA</i> —cont.	
(c) <i>BRACHYURA</i> —cont.	
Crabs . . . . .	38, 40, 41, 47, 57, 58, 61, 70, 74
Cryptochirus . . . . .	74
Cymo andreossi . . . . .	47
Eriphia sebana . . . . .	47
Euplax tridentatus . . . . .	42
Gelasimus . . . . .	42
" annulipes . . . . .	42
" dussumieri . . . . .	41, 42
" tetragonon . . . . .	53, 61
Grapsus strigosus . . . . .	37, 82
Leptodius exaratus . . . . .	59, 61
" nudipes . . . . .	59
Macrophthalmus telescopicus . . . . .	56
Metopograpsus messor . . . . .	42, 59, 61
Ocypode ceratophthalma . . . . .	35
" cordimana . . . . .	35
Percnon abbreviatus . . . . .	86
Phymodius ungulatus . . . . .	44, 59
Pilumnus spinicarpus . . . . .	47
" vespertilio . . . . .	44, 50, 53, 54
Scylla . . . . .	41
" serrata . . . . .	40, 42, 61
Sesarma bidens . . . . .	42, 61
" villosa . . . . .	42, 61
Spider-crabs . . . . .	84
Thalamita admete . . . . .	44, 59
" crenata . . . . .	38, 42, 52
" stimpsoni . . . . .	44, 54
Trapezia cymodoce . . . . .	47
" ferruginea . . . . .	86
Zozymus aeneus . . . . .	86
(v) <i>STOMATOPODA</i> .	
Gonodactylus chiragra . . . . .	44, 59, 74
Lysiosquilla maculata . . . . .	56, 74
Squilla . . . . .	84
Stomatopoda . . . . .	44, 56, 59, 74
ARACHNIDA.	
Arachnida . . . . .	36, 74
Desis crosslandi . . . . .	74
Isometrus maculatus . . . . .	36
Scorpions . . . . .	36
Spiders . . . . .	36, 74
INSECTA.	
Ants . . . . .	36, 40, 41, 57, 61
Beetles . . . . .	36
Butterflies . . . . .	36
Cockroaches . . . . .	36
Danaida melissa subsp. hamata . . . . .	36
Flies . . . . .	36, 40
Grasshoppers . . . . .	36

ARTHROPODA—*cont.*

INSECTA— <i>cont.</i>	PAGE
Insecta . . . . .	42, 61
Mosquitoes . . . . .	36, 42
Moths . . . . .	36
Musca domestica . . . . .	36
Oecophylla smaragdina subsp. virescens	40-42
Pheidole variabilis . . . . .	36
Polyrhachis sokolova . . . . .	40, 42
Sandflies . . . . .	36, 40, 42
Troides priamus subsp. euphorion . . . . .	41
Valanga irregularis . . . . .	36

## MOLLUSCA.

Mollusca . . . . .	37, 56, 58, 67, 70, 74, 80, 89
AMPHINEURA.	
Acanthozostera gemmata . . . . .	37, 44, 53, 61, 74
Amphineura . . . . .	44, 59, 61, 74
Chiton . . . . .	38
Schizochiton incisus . . . . .	44, 59
GASTROPODA.	
Aplysia . . . . .	74, 90
Baler-shell . . . . .	74
Bembicium melanostoma . . . . .	42, 61
Cerithium patulum . . . . .	42
Clava vertagus . . . . .	56, 86
Conus . . . . .	74
,, lividus . . . . .	86
,, marmoreus . . . . .	86
,, striatus . . . . .	86
,, vexillum . . . . .	86
Cypraea . . . . .	74
,, annulus . . . . .	44, 50, 59
,, erroneus . . . . .	44, 59
,, lynx . . . . .	86
,, moneta . . . . .	44, 86
,, tigris . . . . .	81
Dolabella scapula . . . . .	74
Drupa cornus . . . . .	86
,, marginalba . . . . .	59
,, ricinus . . . . .	86
,, rubus-caesius . . . . .	86
,, tuberculata . . . . .	59
Euthyneura . . . . .	74
Gastropoda . . . . .	36, 40, 41, 42, 44, 55-59, 61, 74, 83, 84, 86
Haliotis . . . . .	74
Latirus smaragdulus . . . . .	86
Limpets . . . . .	37, 54
Melampus adamsianus . . . . .	42
,, granifer . . . . .	42
Melarhapse . . . . .	38, 39, 52
,, coccinea . . . . .	80
,, scabra . . . . .	42, 61
,, undulata . . . . .	42, 61, 80
Melo diadema . . . . .	44, 74

MOLLUSCA—*cont.*

GASTROPODA— <i>cont.</i>	PAGE
Nassarius coronatus . . . . .	56
Natica . . . . .	38, 40
,, gualteriana . . . . .	56
Naticidae . . . . .	42, 56
Nerita . . . . .	58
,, albicilla . . . . .	59, 61, 80
,, chamaeleon . . . . .	59, 80
,, costata . . . . .	82
,, lineata . . . . .	42
,, planospira . . . . .	42
,, plicata . . . . .	42, 59, 61, 80, 82
,, polita . . . . .	59, 80
,, striata . . . . .	42, 59, 61
Nudibranchs . . . . .	74, 90
Onchidium . . . . .	44, 50, 53, 59, 74
Ovula . . . . .	74
Planaxis sulcatus . . . . .	37, 59, 61, 80
Pterocera . . . . .	86
,, crocata . . . . .	44, 52
Pyrazus . . . . .	38, 40, 41
,, palustris . . . . .	39, 42
Pythia nux . . . . .	42
Quoyia decollata . . . . .	42, 61
Siphonaria . . . . .	54, 80
,, denticulata . . . . .	44, 55, 59
Snails . . . . .	38
Strombus gibberulus . . . . .	56
,, luhuanus . . . . .	44, 56
Tectarius malaccanus . . . . .	61, 80
Telescopium . . . . .	38, 40, 41
,, telescopium . . . . .	39, 42
Terebra . . . . .	74
,, affinis . . . . .	74
,, muscaria . . . . .	56
Thais armigera . . . . .	86
Trochus . . . . .	86
,, fenestratus . . . . .	44, 55
,, niloticus . . . . .	44, 59, 67
Turbo nivosus . . . . .	59
,, petholatus . . . . .	59
,, porphyrites . . . . .	59, 61
Uber . . . . .	38
,, flemingianum . . . . .	56
,, mammilla . . . . .	56
Vermetidae . . . . .	37, 44
Whelks . . . . .	39, 41
LAMELLIBRANCHIA	
Arca fusca . . . . .	45, 55, 59
,, imbricata . . . . .	59
Bivalves . . . . .	38
Boring lamellibranchs . . . . .	37, 60, 74
Cardium oxygonum . . . . .	56
Chama . . . . .	54
,, jukesii . . . . .	37, 45, 53, 55
Clams . . . . .	38, 47, 62, 64, 83-85, 88, 98, 99

## MOLLUSCA—cont.

LAMELLIBRANCHIA—cont.		PAGE
Cockles . . . . .		38
Corbis fimbriata . . . . .		56
Cyrena coaxans . . . . .		40, 42
Davila plana . . . . .		35
Gafrarium pectinatum . . . . .		38, 42
„ tumidum . . . . .		38, 42
Gastrochaena . . . . .		60, 74
„ gigantea . . . . .		59
Hippopus . . . . .		56, 74, 85
„ hippopus . . . . .	39, 45, 48, 49, 54, 55,	86
Isognoma isognomum . . . . .		45
Lamellibranchs . . . . .	35, 36, 42, 45, 55, 56, 58, 59,	74, 86
Lima tenera . . . . .		45, 55, 75
Lithophaga . . . . .		45, 60, 74
„ argentea . . . . .		59
„ cumingiana . . . . .		59
„ obesa . . . . .		59
„ subula . . . . .		59
„ teres . . . . .		59
Loripes edentulus . . . . .		56
Mactra maculata . . . . .		56
Melina nucleus . . . . .		59
Modiolus auriculatus . . . . .		45, 53, 59
„ cinnamomeus . . . . .		60
Mussels . . . . .		70
Ostrea cerata . . . . .		45
„ crista-galli . . . . .		45
„ mordax . . . . .	36, 40, 42, 45, 52, 59, 60, 70	
Oysters . . . . .		36, 37, 39, 84
Petricola lapicida . . . . .		60
Pinctada margaritifera . . . . .		45, 55, 67
Pinna vexillum . . . . .		52
Spondylus . . . . .		54
„ ducalis . . . . .		45, 53, 55
Tellina palatam . . . . .		42
„ remies . . . . .		42
„ virgata . . . . .		56
Teredo . . . . .		38, 39, 42
Tridacna . . . . .		74
„ crocea . . . . .	39, 45, 47, 59, 60, 67, 74, 85,	86, 89
„ derasa . . . . .	47, 67, 85, 86, 88, 89	
„ elongata . . . . .	85, 86, 88, 89	
„ fossor . . . . .	39, 45, 47, 48, 67, 85, 86, 89, 90	
„ squamosa . . . . .		48

## CEPHALOPODA.

Cephalopoda . . . . .	74
Nautilus . . . . .	74
Octopods . . . . .	74
Sepioteuthis . . . . .	74
Spirula . . . . .	74
Squids . . . . .	74

## ECHINODERMATA.

Echinodermata . . . . .	55, 56, 58, 59, 67, 70, 75, 79, 86, 89
-------------------------	--

## ECHINODERMATA—cont.

ASTEROIDEA.		PAGE
Archaster typicus . . . . .		56, 75
Asterina exigua . . . . .		58, 59, 75
Asteroidea . . . . .		45, 75
Asterope carinifera . . . . .		77
Culcita novae-guineae . . . . .		45, 75
Echinaster luzonicus . . . . .		77
Iconaster longimanus . . . . .		77
Linckia guildingii . . . . .		84-86
„ laevigata . . . . .	45, 48, 67, 75, 84-86, 89	
Nardoa pauciforis . . . . .		45, 75, 86
Oreaster nodosus . . . . .		77

ECHINOIDEA.		PAGE
Centrechinus setosus . . . . .		45, 48, 75
Diadema ; see Centrechinus.		
Echinoidea . . . . .		45, 75
Echinometra mathaei . . . . .	45, 47, 58, 59, 75, 83, 85,	86, 89, 90
Echinostrephus molare . . . . .		67, 83, 86
Laganum depressum . . . . .		56
Tripneustes gratilla . . . . .		45, 75

CRINOIDEA.		PAGE
Comatulids . . . . .		76
Crinoidea . . . . .		67, 75, 85, 86, 89
Lamprometra gyges . . . . .		67

HOLOTHUROIDEA.		PAGE
Holothuria arenicola . . . . .		56
„ argus . . . . .		39, 52
„ atra . . . . .		45, 50, 53, 55
„ coluber . . . . .		45, 48, 55
„ erinaceus . . . . .		59
„ impatiens . . . . .		55
„ leucospilota . . . . .	39, 45, 48, 50,	55, 59, 76
„ marmorata . . . . .		77
„ pardalis . . . . .		59
„ scabra . . . . .		38
Holothurians . . . . .	38, 42, 50, 58, 59, 62, 76, 84, 86	
Holothuroidea . . . . .		45, 76
Polycheira rufescens . . . . .		59
Stichopus chloronotus . . . . .	45, 48, 67, 84, 86, 87	
„ horrens . . . . .		55
Synapta maculata . . . . .		39, 45, 52

OPHIUROIDEA.		PAGE
Ophiactis savignyi . . . . .		77
Ophiarachnella gorgonia . . . . .		77
Ophiarthrum elegans . . . . .		45
„ pictum . . . . .		77
Ophiocoma brevipes var. variegata . . . . .		77
„ scolopendrina . . . . .	45, 49, 53, 59, 75	
Ophiolepis superba . . . . .		77
Ophiothrix longipeda . . . . .		45, 55, 75
Ophiuroidea . . . . .		45, 75

POLYZOA.		PAGE
Polyzoa . . . . .		76
Retepora graeffei . . . . .		76

BRACHIOPODA.		PAGE
Brachiopoda . . . . .		76
Lingula . . . . .		76

ASCIDIACEA.		PAGE
Asciaceae . . . . .	45, 55, 59, 76, 86	
Ascidians . . . . .		39, 42
Botryllus magnicoecus . . . . .		86
Chorizocarpa sydneyensis . . . . .		84, 86
Compound Ascidians . . . . .	38, 39, 76, 83, 84	
Didemnum . . . . .		39
„ candidum . . . . .	45, 55, 59, 76	
„ psammatodes var. skeati . . . . .	55, 76	
Diplosoma virens . . . . .	39, 45, 48, 76, 89, 90	
Simple Ascidians . . . . .		76

ENTEROPNEUSTA.		PAGE
Balanoglossus carnosus . . . . .		56
Enteropneusta . . . . .		56, 76
Ptychodera flava . . . . .		56

PISCES.		PAGE
Actinicola percula . . . . .		47
Amphiprion bicinctus . . . . .		47
Chiloscyllium ocellatum . . . . .		77

PISCES—cont.		PAGE
Commensals . . . . .		47, 66, 72
Fishes . . . . .	38, 47, 66, 70, 77, 85, 89, 98	
Himantura granulata . . . . .		77
Periophthalmus . . . . .		41
„ koelreuteri var. argentil- neatus . . . . .		40, 42
Pisces . . . . .		42
Pranesus ogilbyi . . . . .		77
Pseudomugil signifer . . . . .		77
Rays . . . . .		77, 89
Scomberomorus commerson . . . . .		77
Sharks . . . . .		77
Synanceja horrida . . . . .		77
Taeniura lymma halgani . . . . .		77
Tetrodon hispidus . . . . .		77
Zenarchopterus dispar . . . . .		39

REPTILIA.		PAGE
Geckos . . . . .		40-42, 77
Sea-snakes . . . . .		77

AVES.		PAGE
Birds . . . . .		77
Cuncuma leucogaster . . . . .		77
Demiegretta sacra . . . . .		77
Hérons . . . . .		77
Myristicivora bicolor subsp. spilorrhoea . . . . .		77
Pigeons . . . . .		77
Sea Eagles . . . . .		77

## PLANTS.

BACTERIA.		PAGE
Bacteria . . . . .		71

CRYPTOGAMS.		PAGE
ALGAE.		
Algae . . . . .	48, 54, 58, 62, 64-66, 70, 84-86, 89-91	
(i) PROTOPHYTA.		
Zooxanthellae . . . . .		70
(ii) DIATOMACEAE.		
Diatoms . . . . .		52, 70
(iii) CYANOPHYCEAE.		
Blue-green algae, 36 ; see also Cyanophyceae.		
Cyanophyceae . . . . .	38, 40, 42, 45, 52, 55, 68, 69, 82, 90	
Hormothamnium solutum . . . . .		45, 55
Lyngbya majuscula . . . . .		45, 55, 64
Trichodesmium . . . . .		46
(iv) FLORIDEAE.		
Acanthophora spicifera . . . . .		45, 48
Amphiroa fragilissima . . . . .		45, 49, 68, 89, 90

## CRYPTOGAMS—cont.

ALGAE—cont.		PAGE
(iv) FLORIDEAE—cont.		
Digenia simplex . . . . .		45, 48, 68
Florideae . . . . .		45, 68
Galaxaura . . . . .		49, 68, 90
Laurencia . . . . .		50, 53, 54, 90
„ botryoides . . . . .		45, 48, 68
„ papillosa . . . . .		45, 48, 68
Lithothamnion, 46, 92 ; see also Melobesieae and Nullipores.		
Melobesieae . . . . .	45, 46, 68, 69, 84, 86, 90, 92, 99	
Nullipores . . . . .	46, 47, 54, 57, 58, 69, 83-85, 91	
Polysiphonia . . . . .		48, 55
Red algae, 48 ; see also Florideae.		
Spyridia filamentosa . . . . .		45, 54, 55
Squamariaceae . . . . .		54
(v) PHAEOPHYCEAE.		
Brown algae, 48 ; see also Phaeophyceae.		
Cystophora . . . . .		69
Cystophyllum . . . . .		46, 55, 69

CRYPTOGAMS—*cont.*ALGAE—*cont.*

PAGE

(v) PHAEOPHYCEAE—*cont.*

Cystophyllum muricatum . . . . .	45, 52
Dictyota Bartayresiana . . . . .	45, 68
,, ciliata . . . . .	45, 68
Ecklonia . . . . .	69
Ectocarpus . . . . .	48, 52
Hydroclathrus . . . . .	54
,, clathratus . . . . .	45, 49
Laminaria . . . . .	69
Padina . . . . .	69
,, australis . . . . .	45, 48, 68
,, Commersonii . . . . .	45, 48, 68
Phaeophyceae . . . . .	45, 68
Sargassum . . . . .	46, 52, 55, 65, 69
,, cristaefolium . . . . .	65, 68
,, lanceolatum . . . . .	45, 52
,, latifolium . . . . .	45
,, tarvum . . . . .	45
Turbinaria . . . . .	69
,, ornata . . . . .	48, 65, 68, 89, 90
,, turbinata . . . . .	45, 48, 52

## (vi) CHLOROPHYCEAE.

Anadyomene . . . . .	54
Avrainvillea erecta . . . . .	55
Boodlea . . . . .	49, 53, 54
,, paradoxa . . . . .	45, 48, 68
Bornetella . . . . .	90
,, nitida . . . . .	45, 68
Caulerpa . . . . .	48, 50, 84-86, 89, 90
,, peltata . . . . .	45
,, racemosa . . . . .	45, 52, 55, 58, 68
,, verticillata . . . . .	38, 39, 42, 52, 98
Chlorodesmis . . . . .	85
,, comosa . . . . .	65, 68, 84, 86
Chlorophyceae . . . . .	45, 68
Dictyosphaeria . . . . .	48, 50, 53, 54, 70, 90
,, favulosa . . . . .	45, 68
,, sericea . . . . .	45, 68
,, Versluysii . . . . .	45, 68
Enteromorpha . . . . .	36, 69
Filamentous algae . . . . .	48
Green algae ; see Chlorophyceae.	
Halicystis . . . . .	70
Halimeda . . . . .	39, 50, 84-86, 90, 91
,, cuneata . . . . .	45, 48, 68
,, opuntia . . . . .	45, 48, 52, 68
,, Tuna . . . . .	68
Valonia . . . . .	70
,, aegagropila . . . . .	52
,, Forbesii . . . . .	48
,, macrophysa . . . . .	70
Valoniaceae . . . . .	70

CRYPTOGAMS—*cont.*

## LICHENES.

PAGE

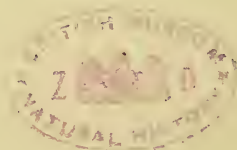
Lichens . . . . .	38, 42
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## FUNGI.

Fungi . . . . .	38, 42
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## PHANEROGAMS.

Achyranthes aspera . . . . .	41, 42
Aegialitis annylata . . . . .	60
Avicennia . . . . .	82, 57
,, officinalis . . . . .	42, 57, 60
Bruguiera Rheedii . . . . .	40, 42
Cassytha filiformis . . . . .	35
Casuarina . . . . .	80
,, equisetifolia . . . . .	35
Cerriops tagal . . . . .	42
Cocos . . . . .	80
,, nucifera . . . . .	35
Commelina cyanea . . . . .	41, 42
Cymodocea . . . . .	89
Diplanthera uninervis . . . . .	49
Euphorbia eremorphila . . . . .	35
Excoecaria agallocha . . . . .	41, 42
Flagellaria indica . . . . .	41, 42
Flowering plants ; see Phanerogams.	
Grass . . . . .	82
Halophila . . . . .	54, 55
,, ovalis . . . . .	45, 52
Ipomoea pes-caprae . . . . .	35
Jasminum simplicifolium . . . . .	35
Josephinia grandiflora . . . . .	80
Lepturus repens . . . . .	41, 42
Mangroves, 24, 25, 27, 37-42, 50, 52, 60, 82, 96, 98 ; see also Avicennia, Bruguiera, Excoecaria, Rhizophara.	
Osbornia octodonta . . . . .	82
Pandanus . . . . .	80, 82
Passiflora foetida . . . . .	35
Pemphis acidula . . . . .	82
Phanerogams . . . . .	42, 45
Premna obtusifolia . . . . .	36
Rhizophora 28, 37, 41, 48, 53, 82 ; see also Mangroves.	
,, mucronata 24, 25, 38, 42, 45, 50, 60	
Scaevola Koenigii . . . . .	35
Sesuvium . . . . .	41, 81, 82
,, Portulacastrum . . . . .	40, 42, 60
Terminalia . . . . .	80
,, catappa . . . . .	35
Thalassia . . . . .	38, 39, 52, 54, 55, 81, 89
,, Hemprichii . . . . .	25, 45, 48, 50
Thespesia populnea . . . . .	41, 42
Tournefortia argentea . . . . .	36
Vigna marina . . . . .	35
Vitex trifolia . . . . .	36





DESCRIPTION OF PLATE I.

Chart of Low Isles.

*Plates I and II reprinted, with some minor corrections, from the 'Geographical Journal,' vol. lxxvi, 1930, by permission of the Royal Geographical Society.*

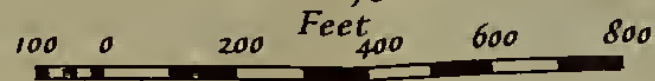
QUEENSLAND

# LOW ISLES

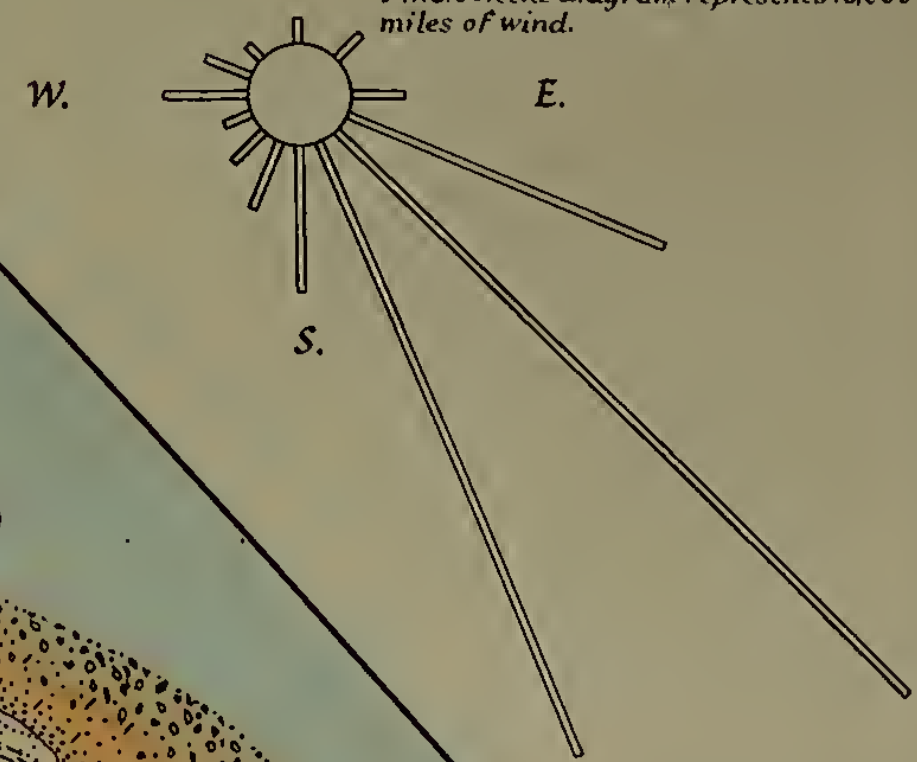
Lat. 16° 23' S. Long. 145° 34' E.

From a survey by M.A. Spender assisted by Mrs. T.A. Stephenson and E.C. Marchant. 1929  
Interior of Mangrove Swamp from photographs by R.A.A.F.

Scale : 1/5000



Wind observations recorded on a Cup Anemometer by A.G. Nicholls. The length of the line on any bearing is the mileage recorded, and represents the amount of wind (that is the product of velocity and the duration of that velocity) over the whole period of 343 days. 1 inch on the diagram represents 10,000 miles of wind.



Outer Rampart Shingle	Mud . . m . . . . .
Inner " "	Rhizophora . . . . .
Shingle . . . . .	Avicennia . . . . .
Boulders . . . . .	Bruguiera etc . . . . .
Sand . . s . . . . .	Dry Vegetation . . . . .
"Honeycomb Rock" . . . . .	Sesuvium . . . . .
Coral . . crl . . . . .	Moats & standing water . . . . .
Basset Edges & Beach Rock . . . . .	Sea . . . . .

Soundings and heights in feet      g. . gravel



DESCRIPTION OF PLATE II.

Chart of Three Isles.

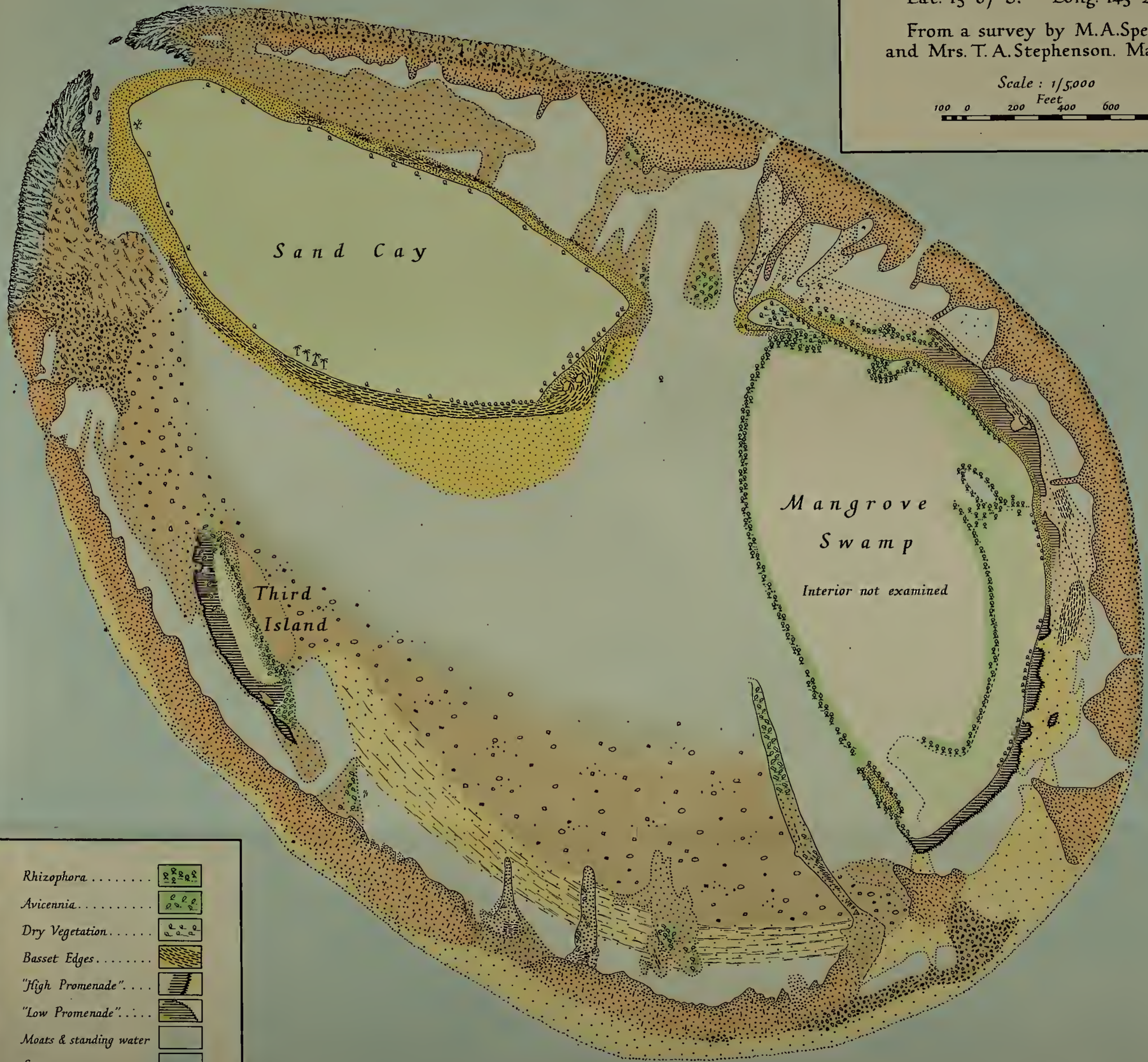
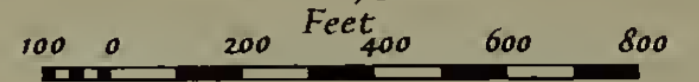
QUEENSLAND

# THREE ISLES

Lat. 15°07' S. Long. 145°25' E.

From a survey by M.A. Spender and Mrs. T.A. Stephenson. May, 1929.

Scale: 1/5,000



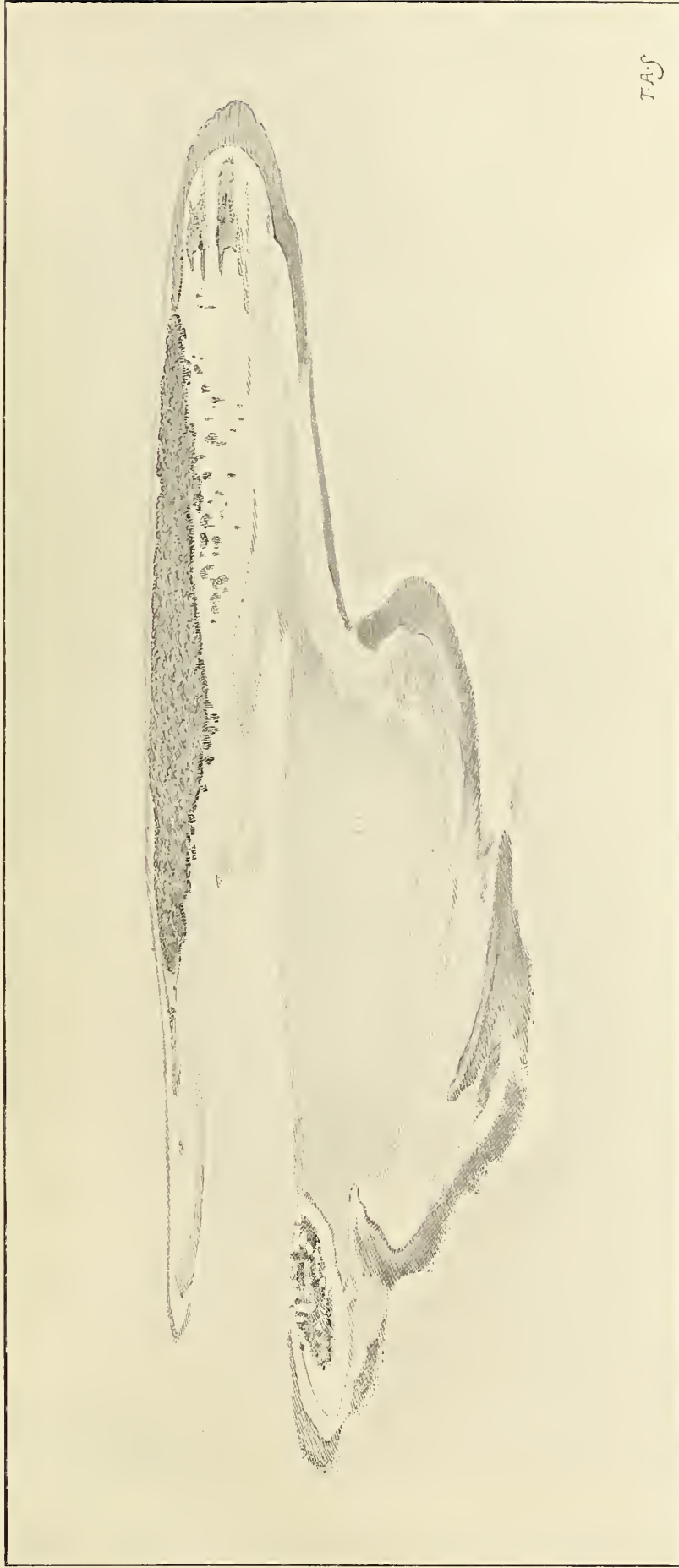
Rampart Shingle . . . . .		Rhizophora . . . . .	
Shingle . . . . .		Avicennia . . . . .	
Shingle and Mud . . . . .		Dry Vegetation . . . . .	
Mud . . . . .		Basset Edges . . . . .	
Boulders . . . . .		"High Promenade" . . . . .	
Sand . . . . .		"Low Promenade" . . . . .	
"Honeycomb Rock" . . . . .		Moats & standing water	
Coral . . . . .		Sea . . . . .	
Palms . . . . .			

### DESCRIPTION OF PLATE III.

#### LOW ISLES.

FIG. 1.—Aerial view of the Low Isles reef, from the westward. The several parts of the reef may be identified by comparison with the coloured map (Plate I). On the cay, the lighthouse and the roofs of the four huts used by the expedition can be seen. The dark patches in the Fungia moat, and between Asterina Spit and the boulder tract, represent areas of coral platform. The sketch was made from a photograph by F. S. Russell, taken from a R.A.A.F. aeroplane, in September 1928.

FIG. 2.—From a second aerial photograph by F. S. Russell, showing the part of the reef concealed by the mangrove swamp in fig. 1. The parts may be identified by reference to Plates I and XXVII. The line representing the seaward edge of the reef is approximate here, as part of it was blurred in the photograph.



*Photo F. S. Russell.*

FIG. 1.



*Photo F. S. Russell.*

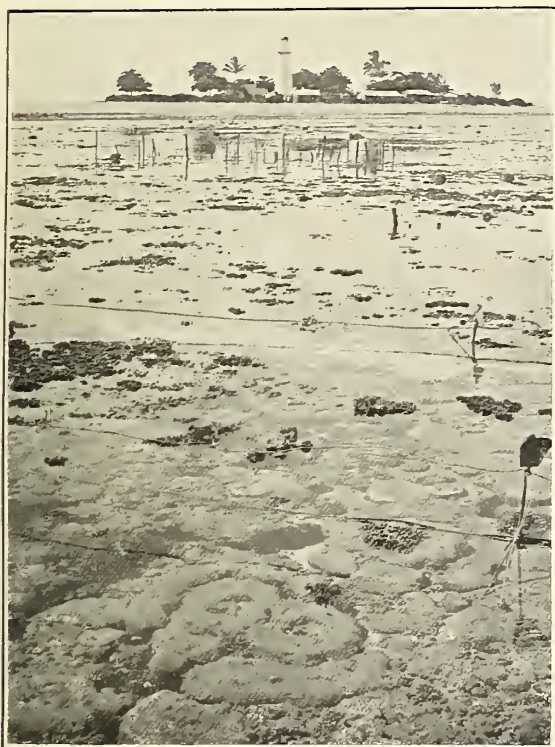
FIG. 2.

## DESCRIPTION OF PLATE IV.

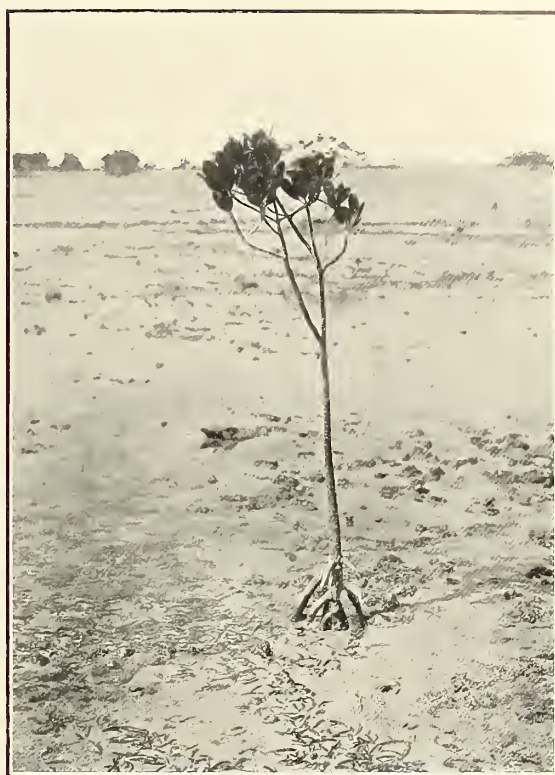
### LOW ISLES.

FIG. 1.—The cay, viewed across the flat at low water, from the western moat. In the foreground the greater part of the moat is occupied by platforms of massive *Porites*, with small pools between. The stakes and wires in the foreground belong to an enclosure made for ecological observations. Those in the middle distance belong to an enclosed pool in which a coral-growth experiment was carried out. The trees visible on the cay are coconut palms, *Terminalia Catappa* and *Casuarina equisetifolia*.

FIGS. 2-4.—These figures illustrate the development of the mangrove *Rhizophora mucronata*. Fig. 3 shows a bunch of seedlings still attached to a twig of the parent tree; the seeds have germinated, and the long green hypocotyls are seen in several stages of development. In fig. 4 a young seedling has established itself in the sand, and in fig. 2 a somewhat older one, growing in the mangrove park, has developed some stilt-roots. In fig. 4 the stilt-roots of adult trees are shown in the background. The grass-like growth in the foreground of fig. 2 is *Thalassia Hemprichii*.



*Photo S. M. Manton.* FIG. 1.



*Photo S. M. Manton.* FIG. 2.



*Photo G. Tandy.* FIG. 3.



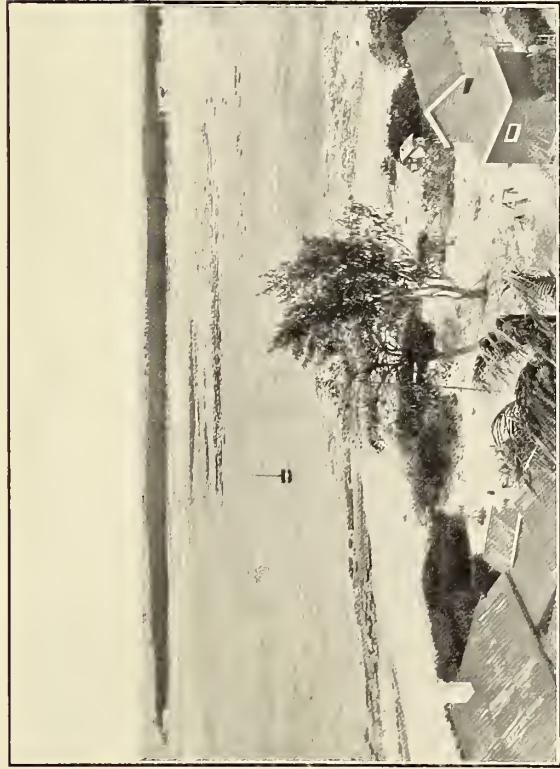
*Photo S. M. Manton.* FIG. 4. *Adlard & Son, Ltd., Impr.*



## DESCRIPTION OF PLATE V.

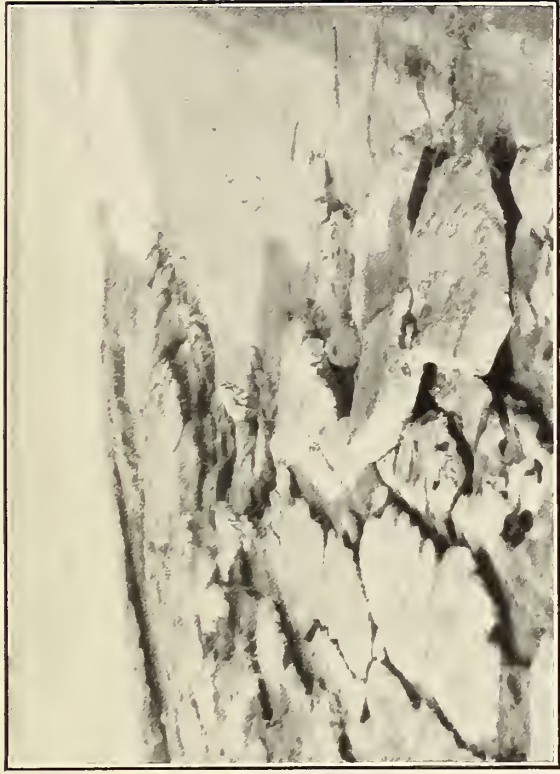
### LOW ISLES.

- FIG. 1.—General view of the mangrove swamp from the top of the lighthouse. Between the shore of the cay (in the foreground) and the swamp lies the anchorage, and in it are seen the reefs marked A4 on the key chart. The time is low water of a spring tide. Fringing the sand of the cay, on the left, is some beach sandstone (C4 and 6). The trees are *Terminalia* and *Casuarina*.
- FIG. 2.—Part of the principal mass of beach sandstone (C6) viewed at close quarters. The loose blocks in the foreground were broken away artificially.
- FIG. 3.—Part of the boulder tract near the letters B2 on the key chart.
- FIG. 4.—A large boulder on the seaward side of the boulder tract. This is the boulder described on p. 36, and the photograph shows the dense masses of rock-oysters (*Ostrea mordax*) which cover its upper part, and the sharp lower limit to which they extend.



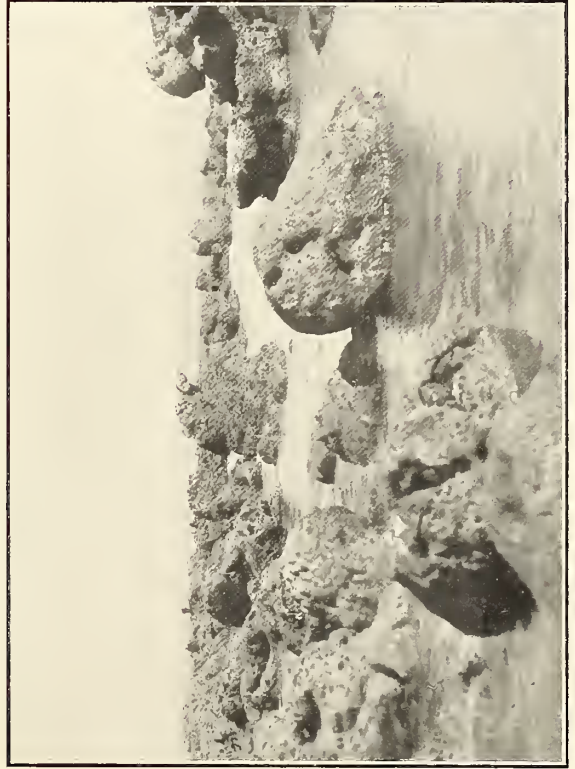
*Photo M. A. Spender.*

FIG. 1.



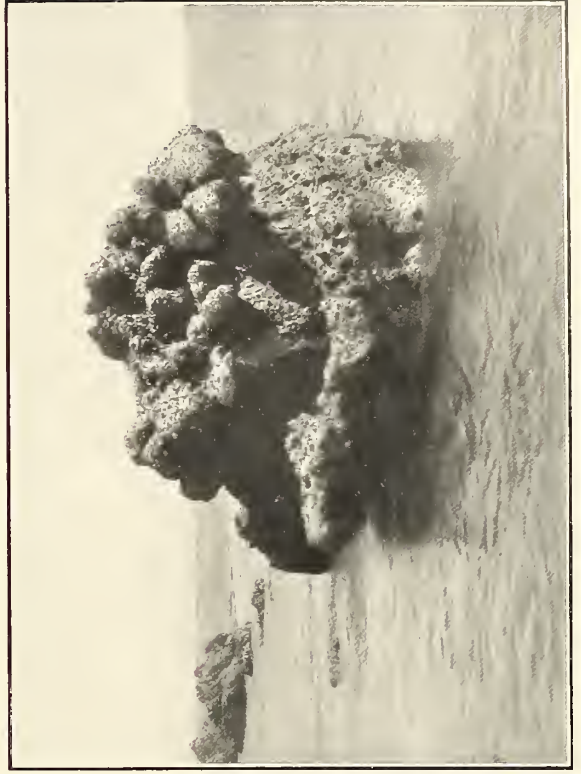
*Photo T. A. Stephenson.*

FIG. 2.



*Photo T. A. Stephenson.*

FIG. 3.



*Photo T. A. Stephenson.*

FIG. 4.

## DESCRIPTION OF PLATE VI.

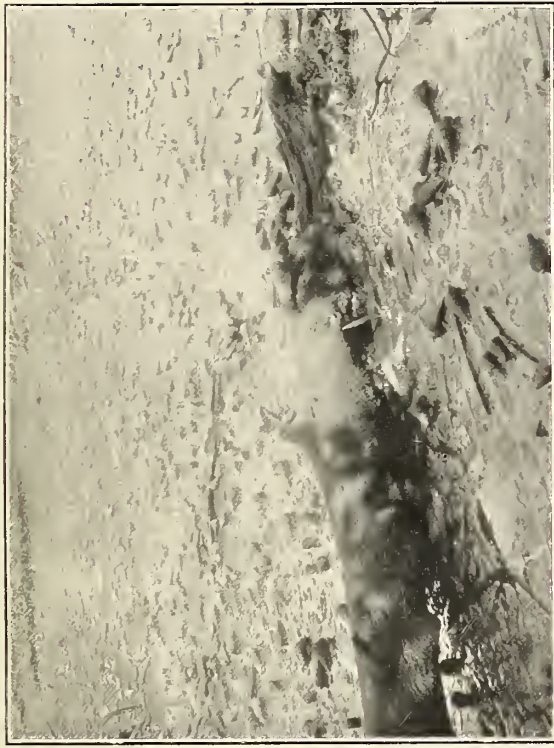
### LOW ISLES.

- FIG. 1.—The muddy glade IM5, in the mangrove swamp, viewed from the edge of the inner rampart at the time of low water. The trees are mostly *Rhizophora*, but there is one small *Avicennia*. The floor is black mud.
- FIG. 2.—The muddy glade IM4, viewed from the shingle-spit IM4B. The whelks which abound on the mud are *Telescopium telescopium* and *Pyrazus palustris*.
- FIG. 3.—Detail of part of a boulder in the boulder tract, showing a number of colonies of a zoanthid belonging to the genus *Palythoa*, exposed in the sun during low water, and two specimens of the boring clam *Tridacna crocea*, partly buried in the rock.
- FIG. 4.—Part of a boulder close to the one illustrated in fig. 3, showing five specimens of *Tridacna crocea*, more completely buried than those shown in fig. 3. The mouths of the burrows of other boring forms are also visible.



*Photo T. A. Stephenson.*

FIG. 1.



*Photo T. A. Stephenson.*

FIG. 2.



*Photo T. A. Stephenson.*

FIG. 3.



*Photo T. A. Stephenson.*

FIG. 4.

## DESCRIPTION OF PLATE VII.

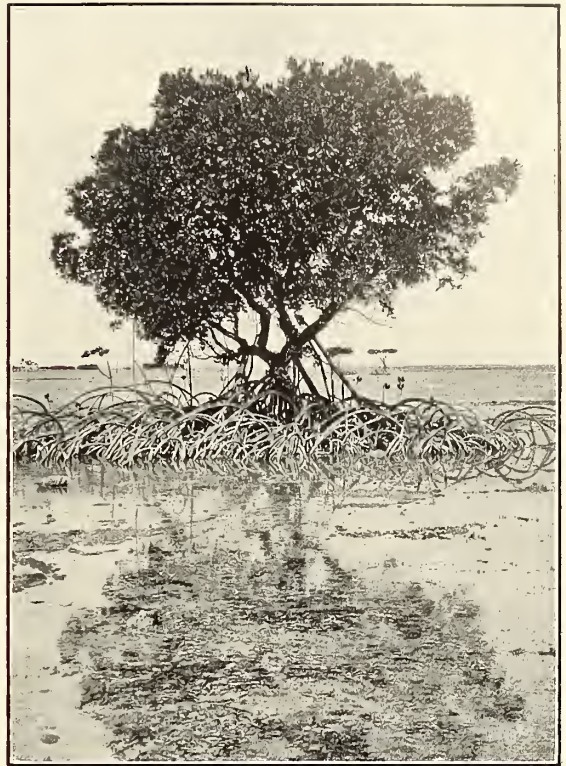
### LOW ISLES AND DAINTREE RIVER.

- FIG. 1.—The vegetation on Green Ant Island; typical dry-land scrub, contrasting with the mangrove-vegetation shown in figs. 2-4.
- FIG. 2.—An isolated adult of *Rhizophora mucronata*, in the mangrove park, showing to full advantage the system of stilt-roots.
- FIG. 3.—To show the general aspect of the dense parts of the mangrove swamp. This photograph was taken near the mouth of the Daintree River, on the mainland, but illustrates the nature of the swamp at Low Isles equally well, except that it includes *Bruguiera*, which is strictly localized at Low Isles.
- FIG. 4.—The sandy pool IM1, inside the swamp. This pool contrasts with those illustrated in Plate VI, figs. 1 and 2, in having a sandy floor covered by water at low tide, instead of a muddy floor exposed at low water.



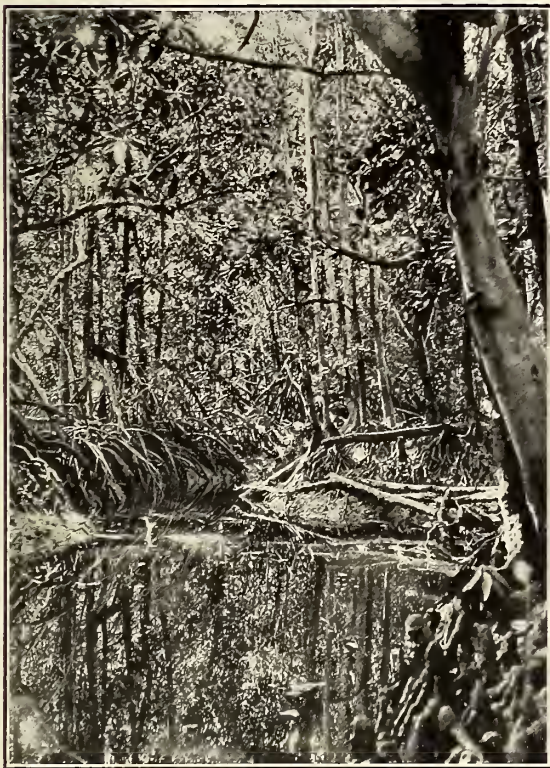
*Photo G. Tandy.*

FIG. 1.



*Photo S. M. Manton.*

FIG. 2.



*Photo S. M. Manton.*

FIG. 3.



*Photo T. A. Stephenson.*

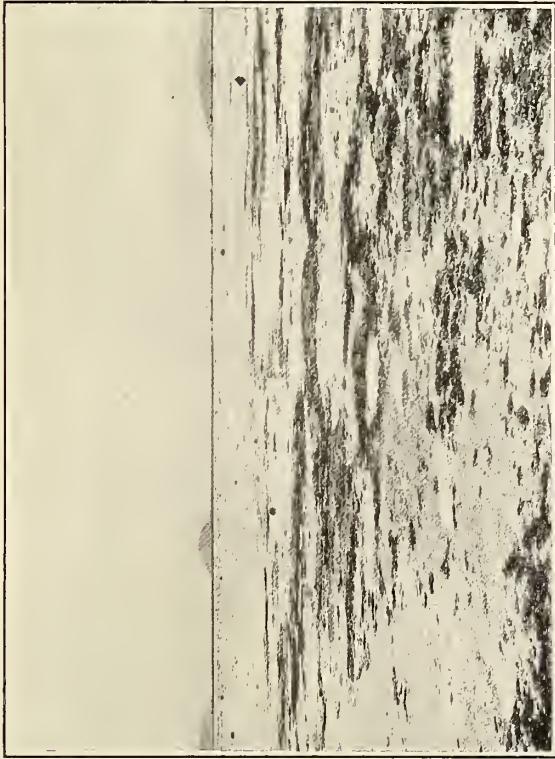
FIG. 4.

*Adlard & Son, Ltd., Impr.*

## DESCRIPTION OF PLATE VIII.

### LOW ISLES.

- FIG. 1.—General view of the sand flat, looking towards the western corner of the reef, with parts of the Thalamita flat, rampart, and boulder tract in the middle distance, and the mainland behind. On the sand are seen numerous mats of the blue-green algae *Lyngbya majuscula* and *Hormothamnium solutum*.
- FIG. 2.—Shallow moat-pools just inside the edge of the outer rampart. The post on the rampart is C beacon (see coloured map).
- FIG. 3.—The madreporite moat, near the gap C, looking seaward. The moat here is occupied by extensive platforms of *Acropora hebes*. The tips of the branches, although they are exposed at low water, are mostly alive in this part of the moat.
- FIG. 4.—A disc-shaped boulder formed by the lateral extension of a colony of massive *Porites*, in shallow water. It is dead except round the edges, and is much encrusted by other organisms.



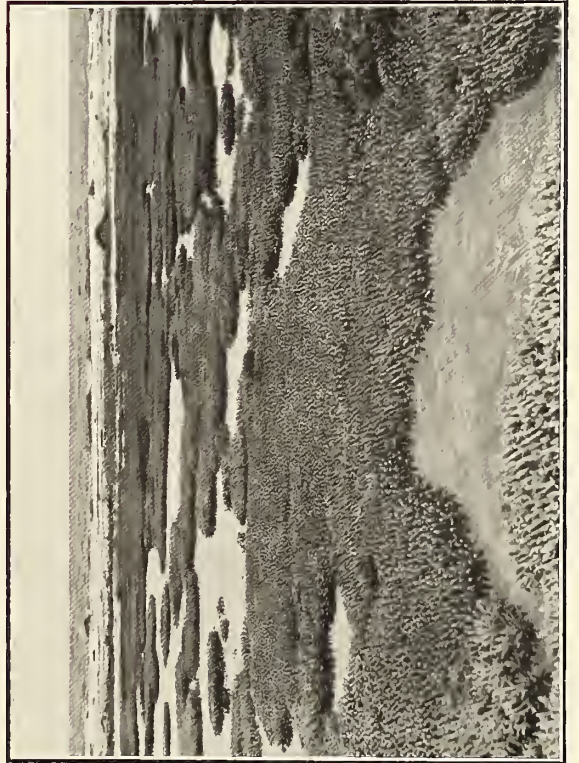
*Photo G. Tandy.*

FIG. 1.



*Photo M. A. Spender.*

FIG. 2.



*Photo T. C. Roughley.*

FIG. 3.



*Photo M. A. Spender.*

FIG. 4.



## DESCRIPTION OF PLATE IX.

### LOW ISLES.

FIG. 1.—The formation of platforms of *Montipora ramosa* in the western moat (see p. 47).

FIG. 2.—Bushes of a coral (*Acropora pulchra*) which is characteristic of a given level on the reef, occurring in situations open to the sea and just above datum level. These bushes were on the seaward side of the area A1 of Luana Reef. The pale organism in the pool is a fleshy alcyonarian (a species of *Sinularia*).

FIGS. 3 and 4.—Details of the coral growth in the western moat. Fig. 3 shows a good deal of dead rock; *Favias*; a *Coeloria*; colonies of *Acropora* (some alive, the rest dead and encrusted); a fringe of living massive *Porites* round the edge of a dead platform; a little foliose *Montipora*; and a small clam. Fig. 4 includes a *Fungia* and a considerable area of *Montipora ramosa* as well as other elements.



Photo T. A. Stephenson.

FIG. 1.

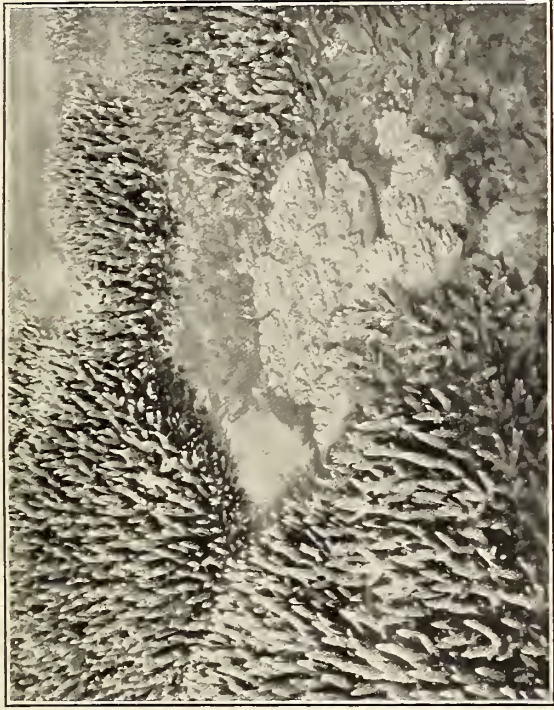


Photo T. A. Stephenson.

FIG. 2.

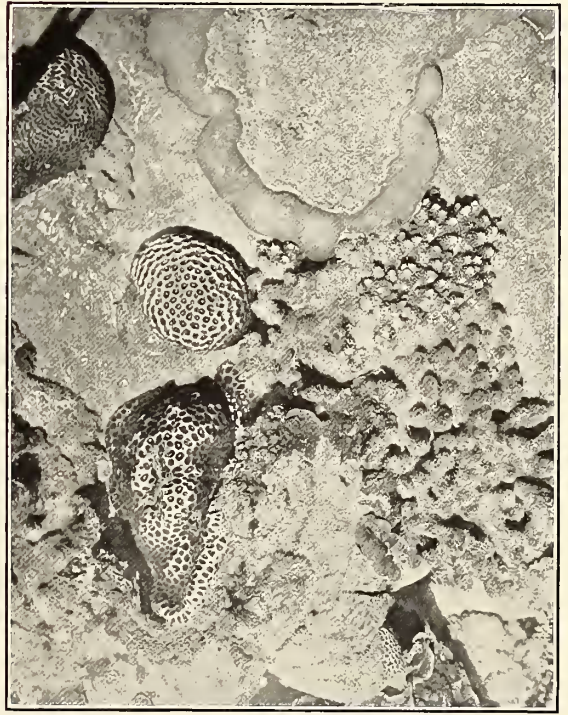


Photo S. M. Manton.

FIG. 3.

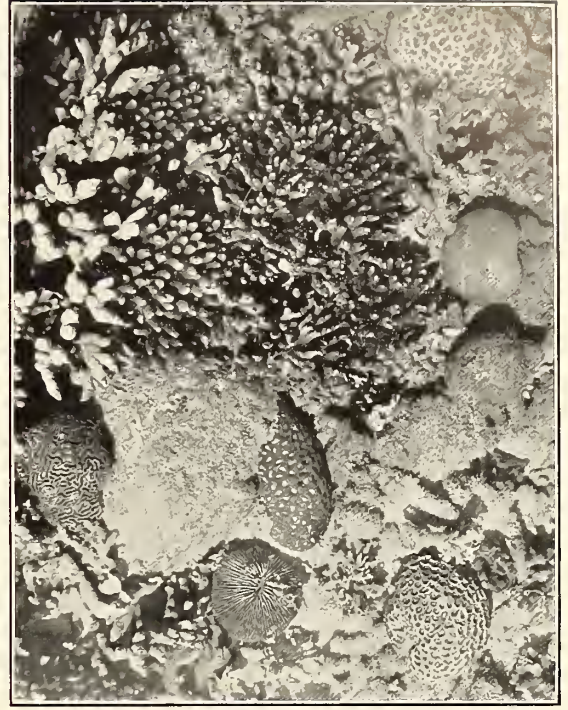


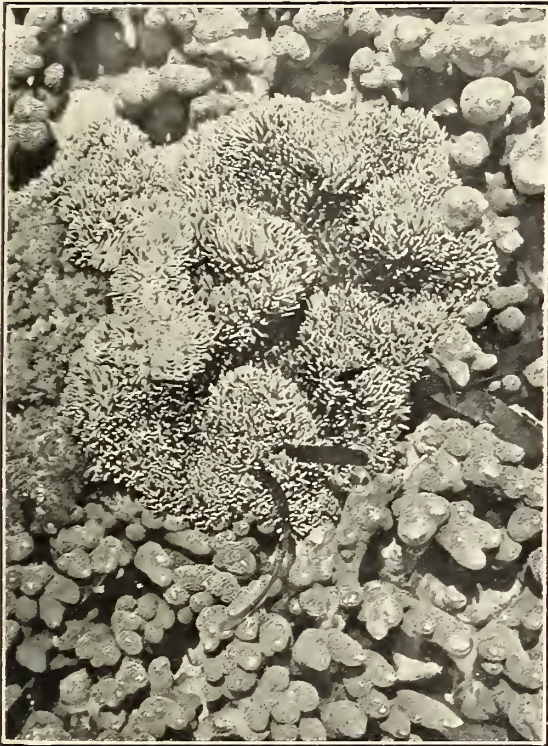
Photo S. M. Manton.

FIG. 4.

## DESCRIPTION OF PLATE X.

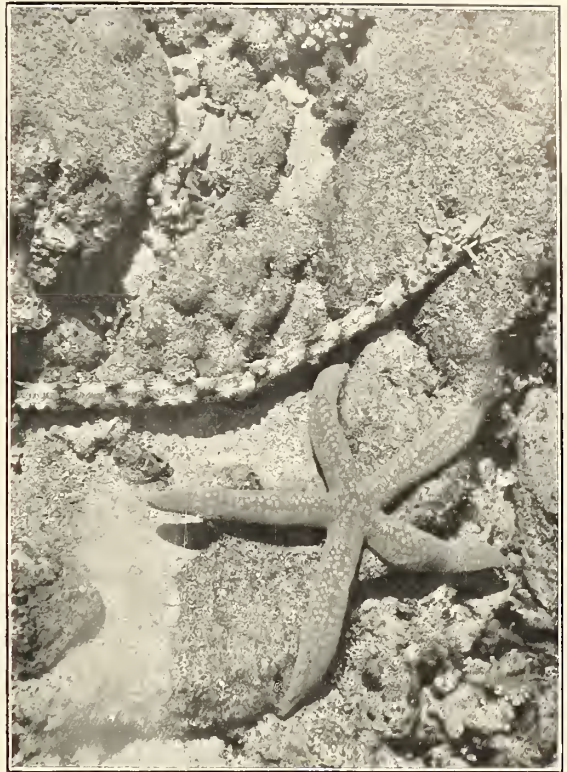
### LOW ISLES.

- FIG. 1.—Western moat. Part of a living platform of *Montipora ramosa* with a dark blue specimen of *Stoichactis kenti*.
- FIG. 2.—*Synapta maculata* (above); head-end of a large specimen, with tentacles expanded; and *Linckia laevigata* (below).
- FIG. 3.—In the moat-pool M7. The urchin is *Echinometra mathaei*, the coral *Montipora ramosa*. Note the small polyps of the latter (visible as a honeycomb pattern), fully expanded in sunlight.
- FIG. 4.—Detail of the top of a platform (in a moat) of branched coral. Much of the coral is dead, and is encrusted by *Melobesia*e and other algae. The grass-like leaves belong to *Thalassia Hemprichii*.



*Photo S. M. Manton.*

FIG. 1.



*Photo S. M. Manton.*

FIG. 2.



*Photo T. A. Stephenson.*

FIG. 3.



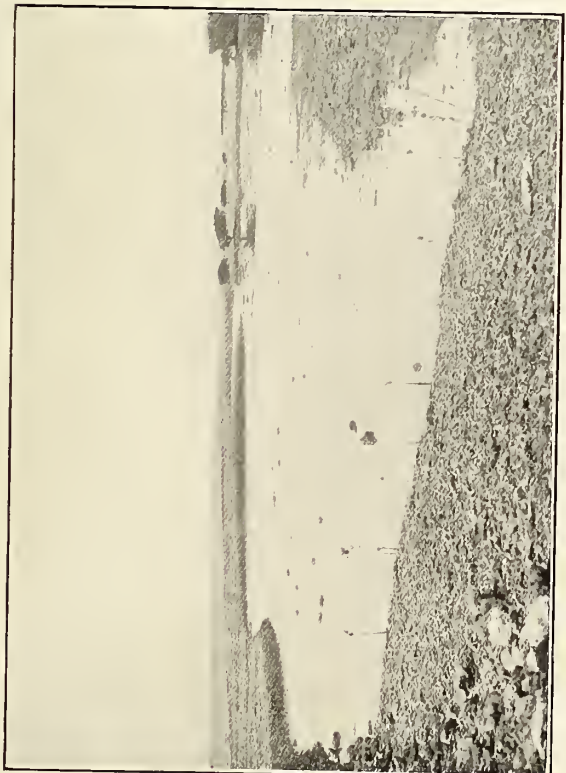
*Photo G. Tandy.*

FIG. 4. *Adlard & Son, Ltd., Impr.*

## DESCRIPTION OF PLATE XI.

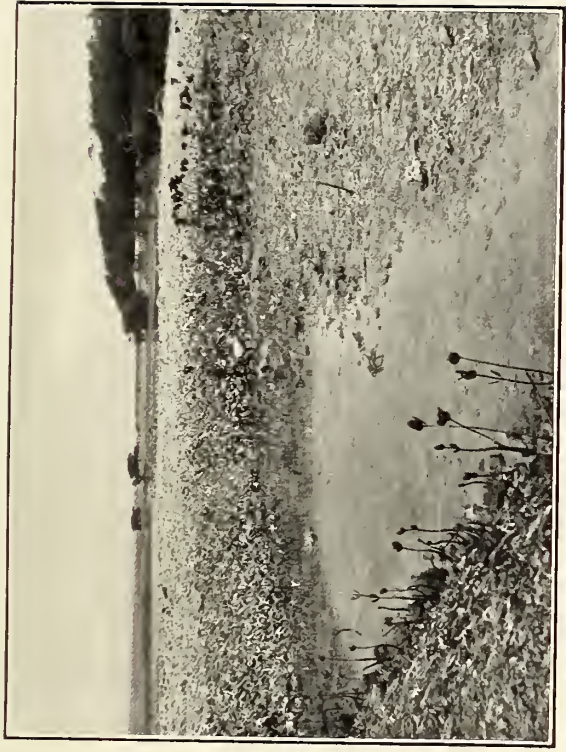
### LOW ISLES.

- FIG. 1.—General view of a portion of the outer rampart, and of the seaward end of the moat-pool M7, looking southward.
- FIG. 2.—The shingle-tongue R5 and the moat-pool M8. Note the steep slope of the shingle escarpment, and the seedlings of *Rhizophora* which have colonized it.
- FIG. 3.—Part of the outer rampart shown in detail. The fragments are all loose. Note the predominance of stick-like pieces belonging to species of *Acropora*.
- FIG. 4.—Showing the encroachment of the dead shingle of the rampart (in the lower part of the figure) upon living coral in the moat.



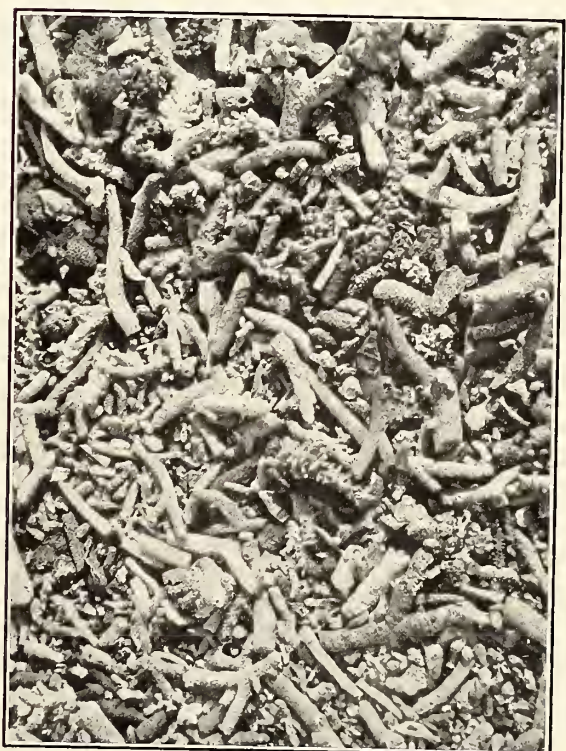
*Photo T. A. Stephenson.*

FIG. 1.



*Photo T. A. Stephenson.*

FIG. 2.



*Photo T. A. Stephenson.*

FIG. 3.



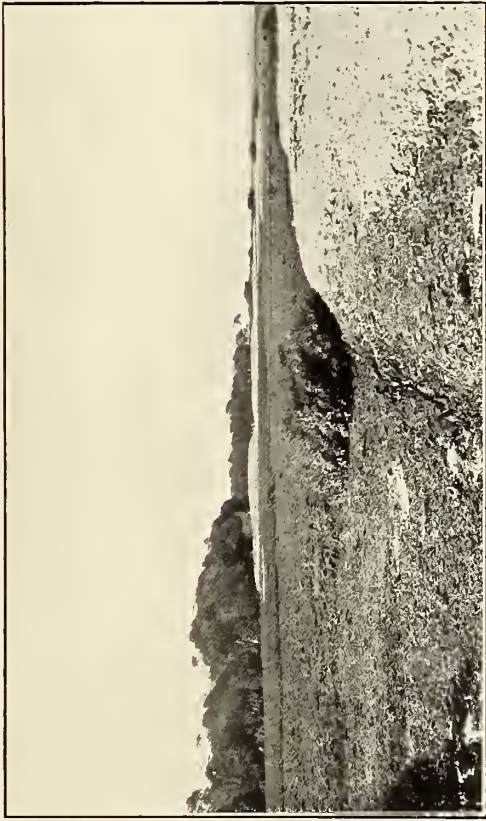
*Photo M. A. Spender.*

FIG. 4.

## DESCRIPTION OF PLATE XII.

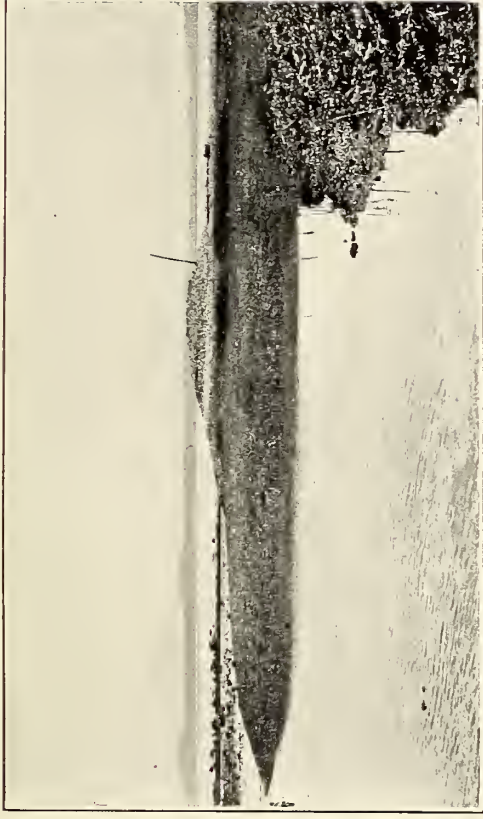
### LOW ISLES.

- FIG. 1.—A view of the inner rampart, looking northward from near the shingle-tongue R6. In the foreground on the right is part of the outer rampart, with its escarpment, and here a new wave of clean shingle is clearly seen encroaching upon the older and dirtier shingle. The bush in the centre of the photograph is the one mentioned on p. 57. The mangrove swamp is on the left.
- FIG. 2.—The shingle mound and part of the north-east moat.
- FIG. 3.—A bush of *Avicennia officinalis* growing on the inner rampart, and showing the characteristic form of growth in this position. Note the pneumatophores growing upward from the substratum.
- FIG. 4.—Part of the inner rampart near the south-eastern extremity of the reef, showing a field of *Sesuvium Portulacastrum*. The bushes on the left are *Rhizophora mucronata*.



*Photo G. Tandy.*

FIG. 1.



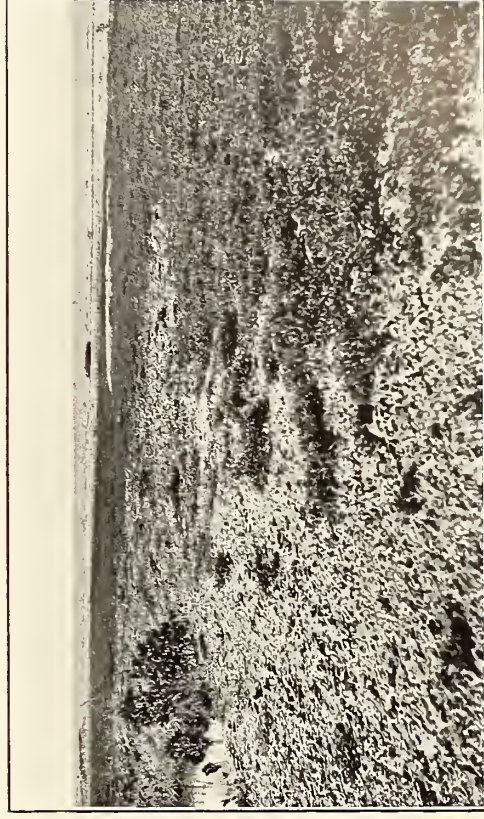
*Photo M. A. Spender.*

FIG. 2.



*Photo S. M. Manton.*

FIG. 3.



*Photo S. M. Manton.*

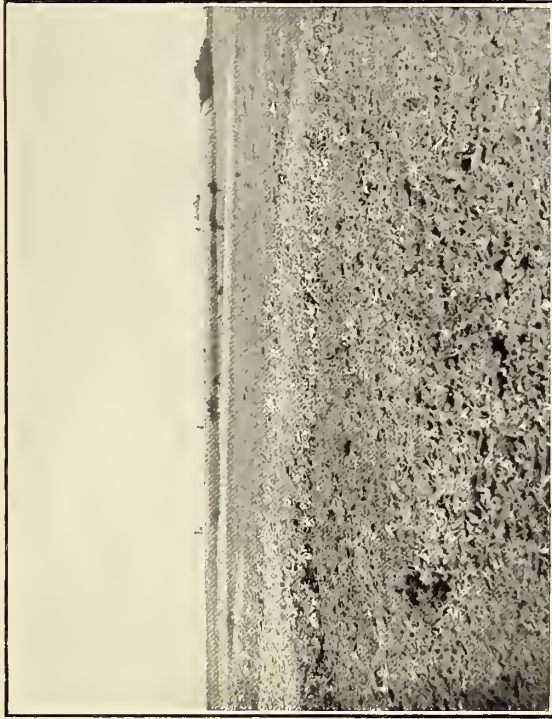
FIG. 4.



## DESCRIPTION OF PLATE XIII.

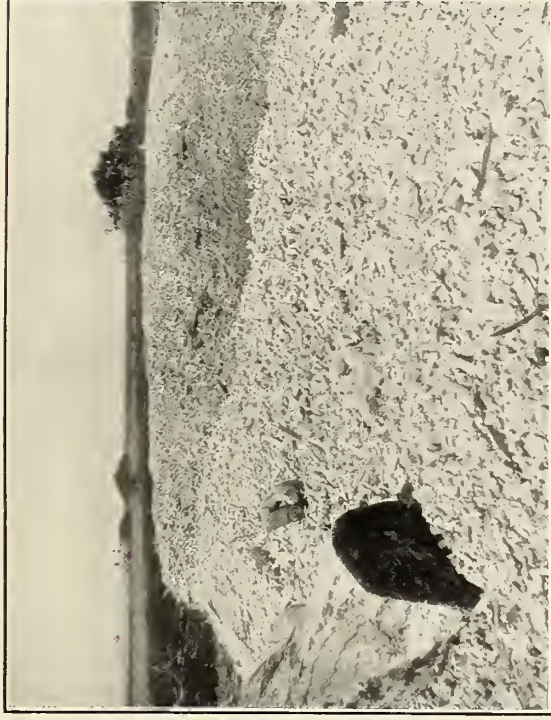
### LOW ISLES.

- FIG. 1.—Two shingle-tongues belonging to the outer rampart (the more distant one is the tongue R2 of the key chart), which have encroached upon the inner rampart.
- FIG. 2.—A semicircular bank of loose shingle which has been piled up at the inner side of the inner rampart, opposite the place marked R3 on the key chart.
- FIG. 3.—Inner edge of the inner rampart, in the northern part of its course, showing dead and dying trees of *Rhizophora*, which are now situated outside the swamp, and which appear to have succumbed to unfavourable conditions.
- FIG. 4.—A corner of the mangrove park—the pool P10 in the foreground, and the escarpment of the inner rampart on the left.



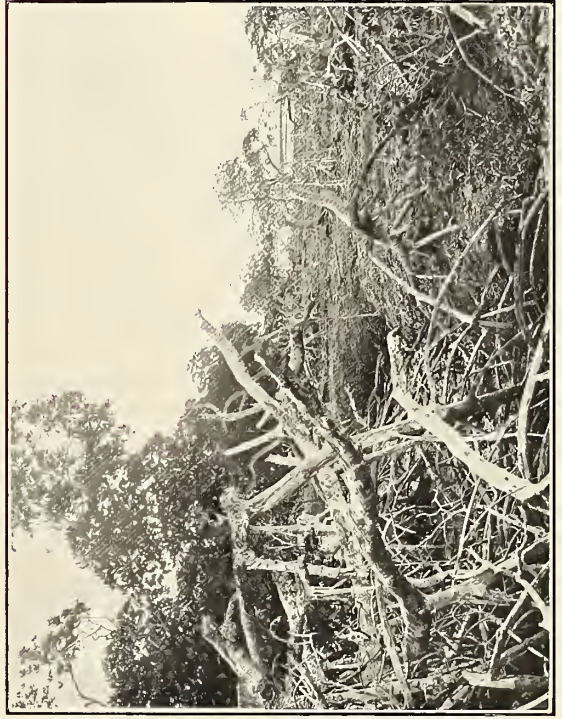
*Photo T. A. Stephenson.*

FIG. 1.



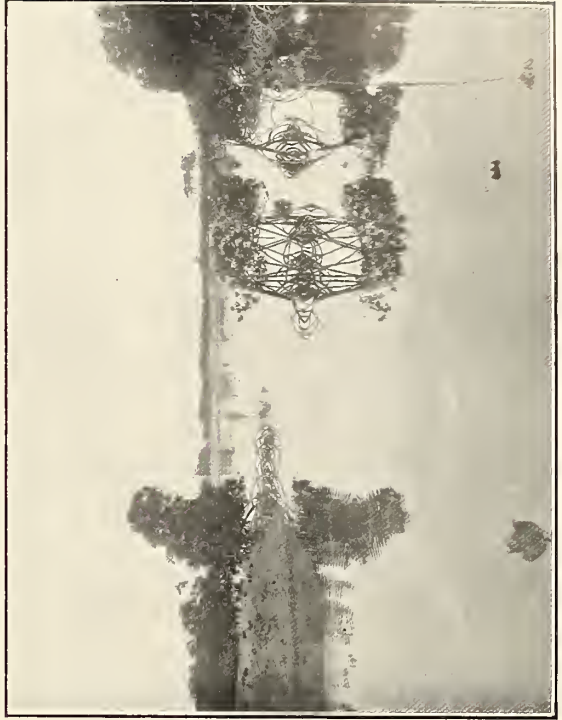
*Photo T. A. Stephenson.*

FIG. 2.



*Photo G. Tandy.*

FIG. 3.



*Photo T. A. Stephenson.*

FIG. 4.

## DESCRIPTION OF PLATE XIV.

### LOW ISLES.

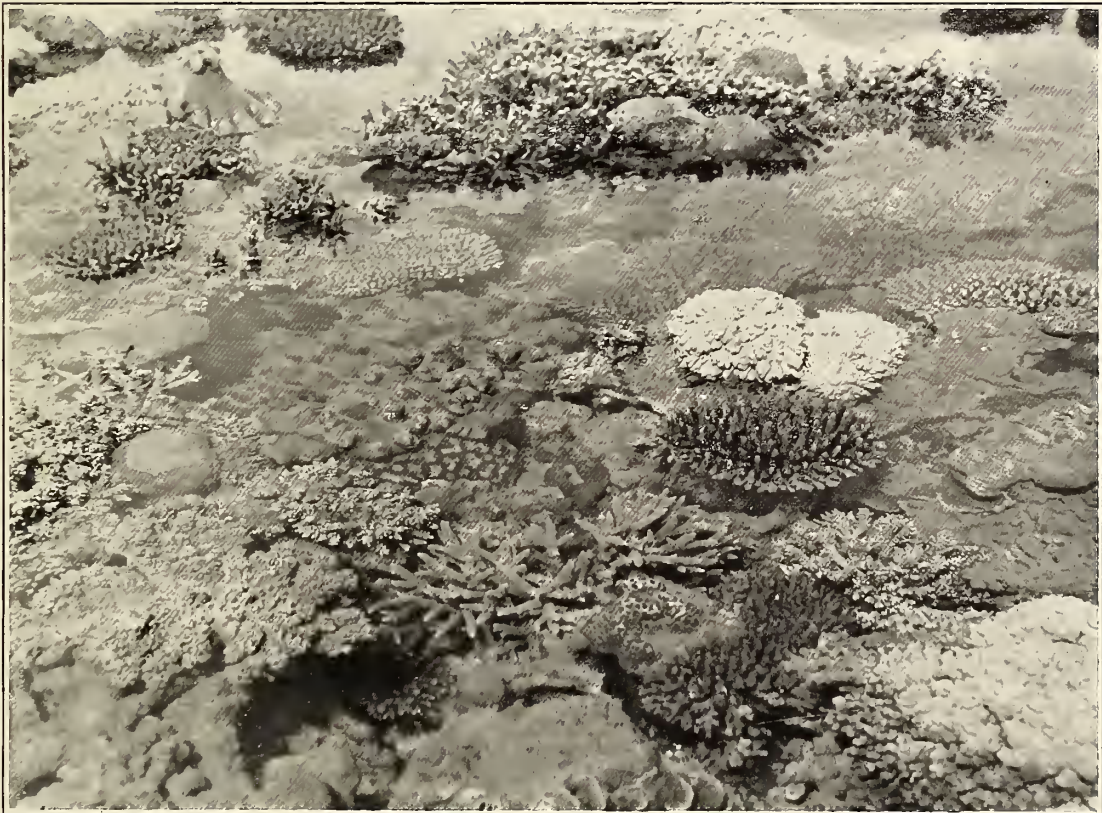
FIG. 1.—Part of the anchorage, viewed from the top of the lighthouse. In the foreground is some beach sandstone, and beyond this the region A1 of Luana Reef. The island-like reef farther away is A3. For further explanation see p. 62.

FIG. 2.—Part of an anchorage reef at close quarters, showing a considerable growth of coral. Among the corals may be seen cyathiform growths of *Acropora*, as well as stagshorn and bush-like species; a colony of *Lobophyllia*; and forms of *Montipora*. There are also alcyonaria (*Sarcophytum* and *Sinularia*).



*Photo M. A. Spender.*

FIG. 1.



*Photo T. C. Roughley.*

FIG. 2.

## DESCRIPTION OF PLATE XV.

### LOW ISLES.

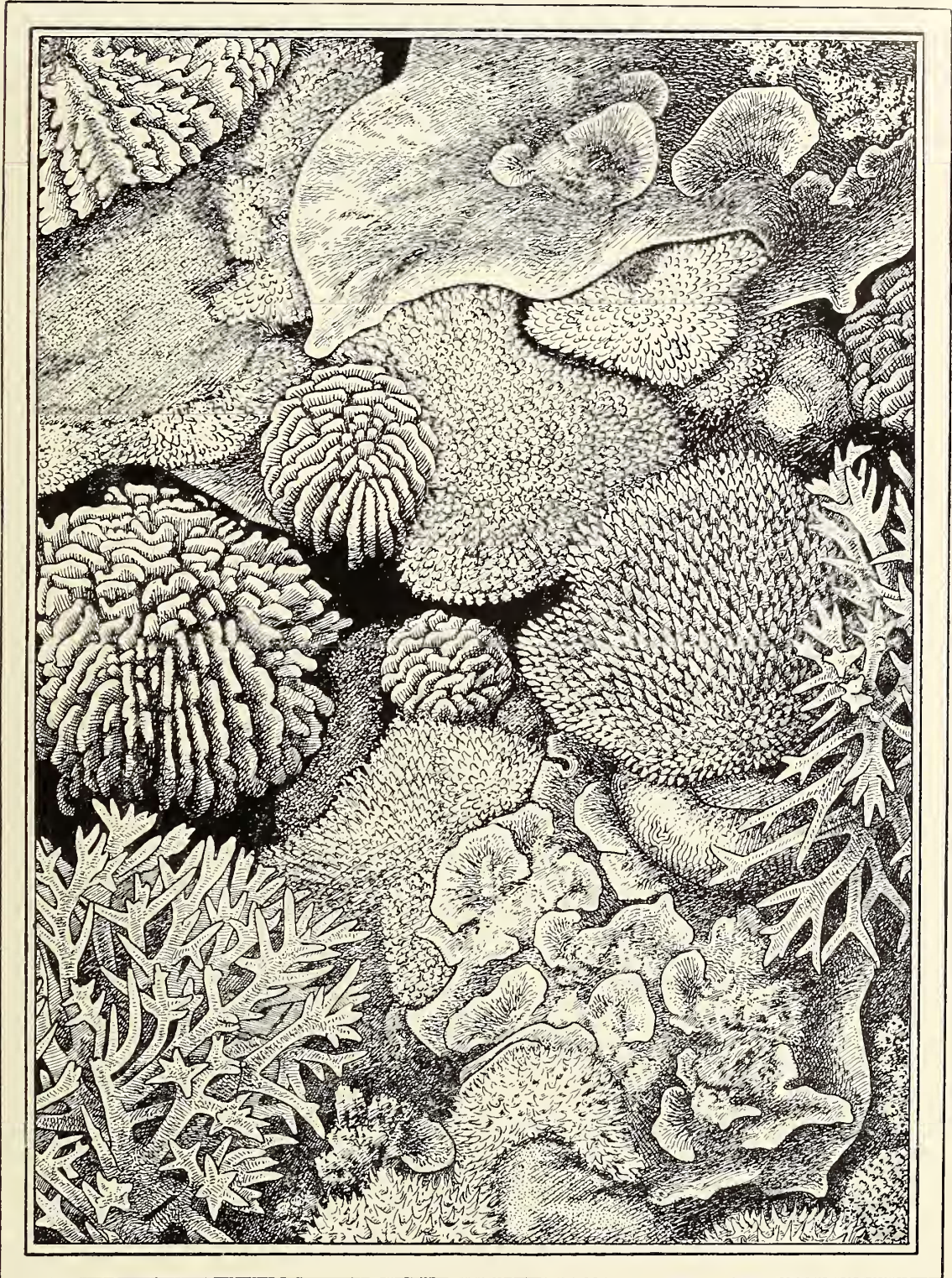
A partially diagrammatic drawing of an area of rich coral growth in the anchorage, towards the edge of the region A2 of Luana Reef. The area was about 8 ft. long by 6 ft. wide. The colonies with radiating vertical lamellae are *Heliopora coerulea*; the coxcomb-like formation in the upper left-hand corner is a species of *Lobophytum*. The foliose forms are species of *Montipora*; the bracket-like growths are species of *Acropora* (mostly *A. squamosa* and *A. loripes*); the stagshorn is also an *Acropora*. At the bottom of the drawing are three colonies of *Seriatopora*, with sharply-pointed branches. A colony of *Coeloria*, partly dead on top, is to be seen on the right, overhung by a stagshorn and a bracket-like madrepora.

GREAT BARRIER REEF EXPEDITION 1928-29.

*Brit. Mus. (Nat. Hist.).*

REPORTS, VOL. III, No. 2.

PLATE XV.



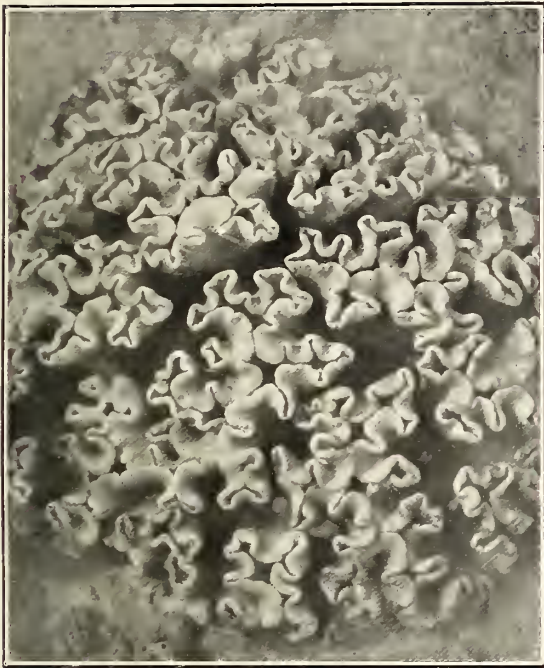
*T.A.S. ad nat. del*

*Acland & Son, Ltd., Impr.*

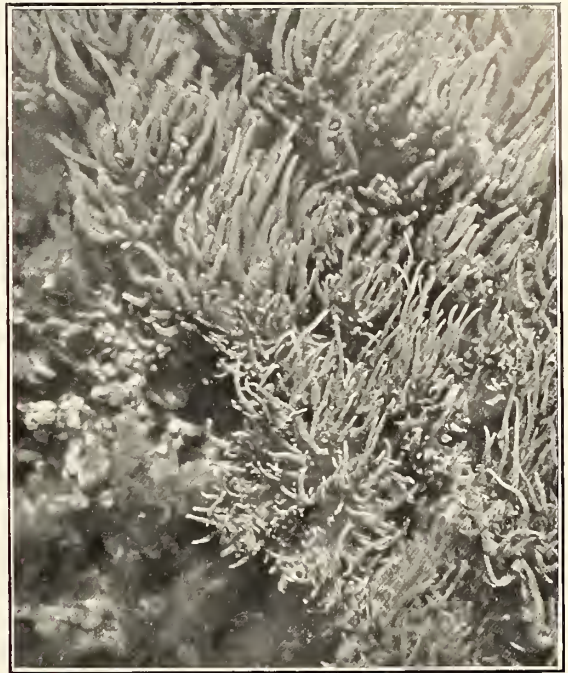
## DESCRIPTION OF PLATE XVI.

### ALCYONARIA AT LOW ISLES.

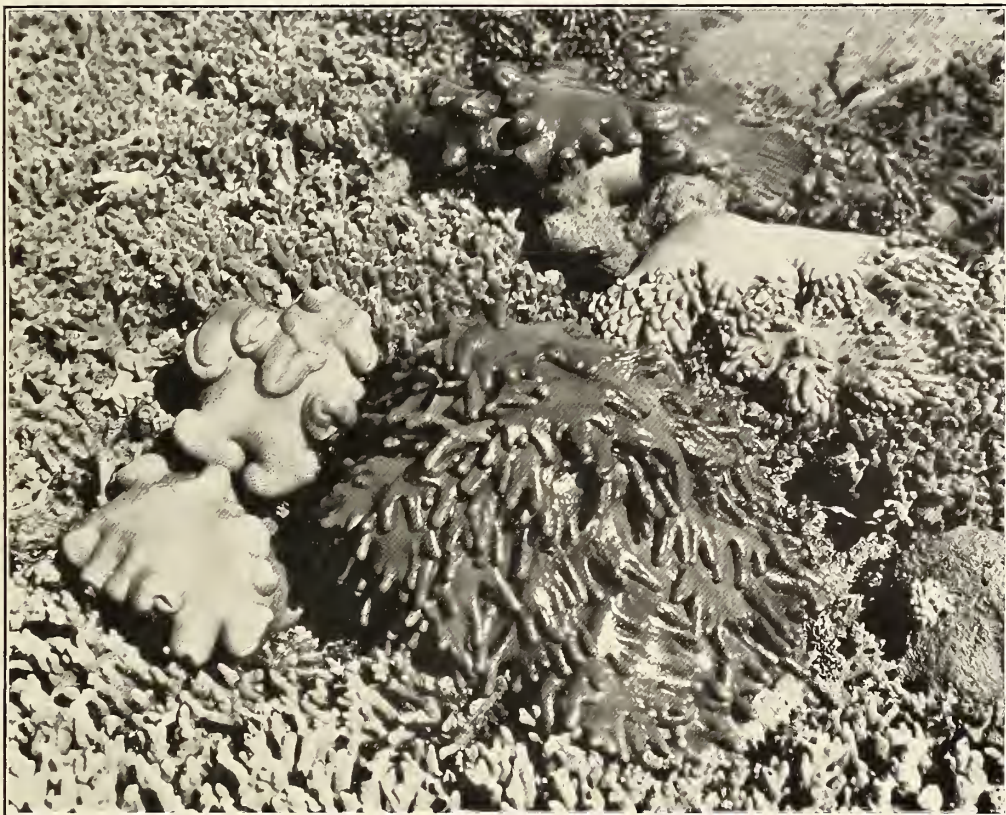
- FIG. 1.—A large colony of *Sarcophytum*, under water. The colour would be yellowish green and the size several feet across.
- FIG. 2.—Part of a field of *Sinularia flexibilis*, under water, in the anchorage. The “tails” are soft, pale brown, and several inches long.
- FIG. 3.—Fleshy alcyonaria (*Sarcophytum*, *Lobophytum* and *Sinularia*), exposed in the sun at low water, in the region A1 of Luana Reef. The branched coral is *Montipora ramosa*.



*Photo T. C. Roughley.* FIG. 1.



*Photo S. M. Manton.* FIG. 2.



*Photo T. C. Roughley.*

FIG. 3.

*Adlard & Son, Ltd., Impr.*

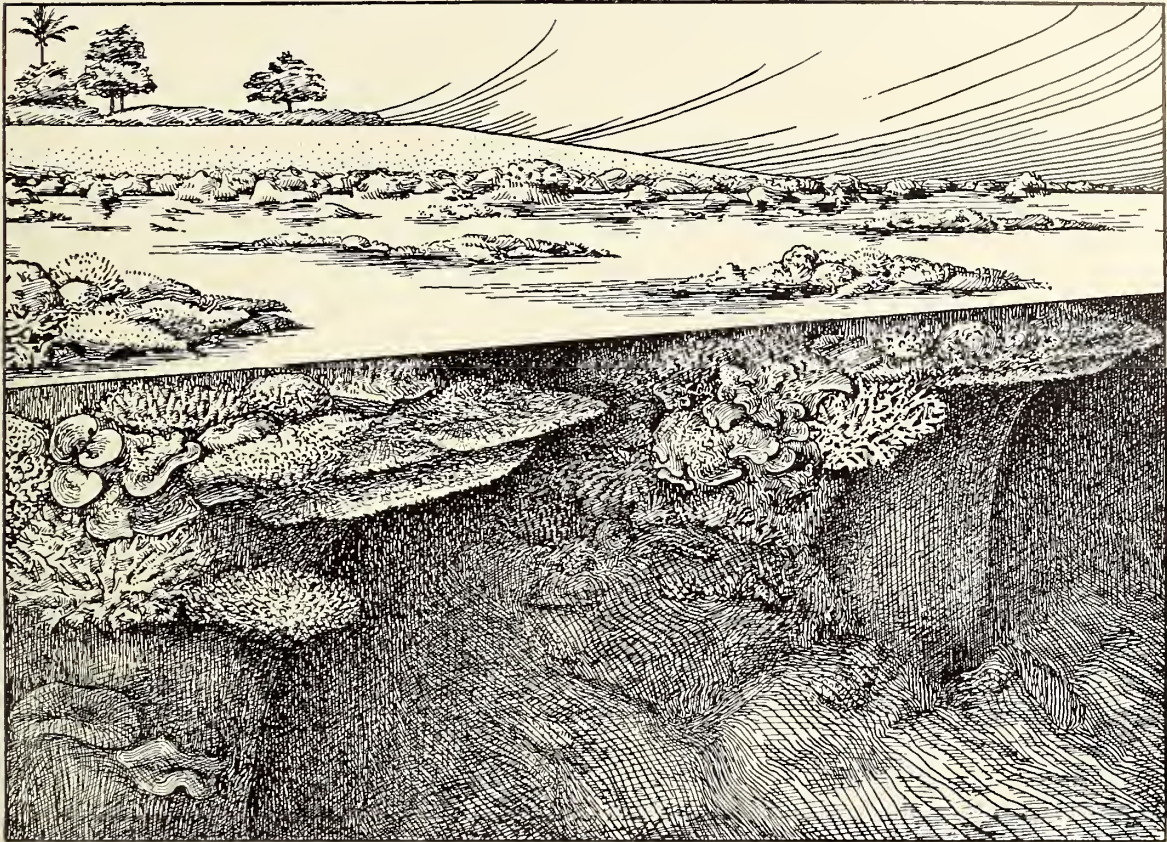


## DESCRIPTION OF PLATE XVII.

### LOW ISLES AND YONGE REEF.

FIG. 1.—Diagram to illustrate the nature of the seaward slope off the leeward side of Low Isles, and the mode of growth of the coral. In the distance is part of the cay; in front of it a portion of the boulder tract; and in the foreground are two coral heads showing the overhanging form which they often assume, and the manner in which the principal growth of corals is to be found on top of them and a little below the top. In the case of the coral head on the right-hand side of the foreground, the slope from the top of the head to the level of the sea-floor is gradual on one side; and here the rich growth of coral extends farther down than on the overhanging surface. The proportions in this diagram should not be taken too seriously, and it should be compared with Text-fig. 10 and with the text (p. 65). The time is that of low water of a low spring tide.

FIG. 2.—Diagram to illustrate the arrangement of the several zones on Yonge Reef. This should be compared with the text (p. 30) and with Text-fig. 5. The figure is drawn as far as possible to scale, the vertical scale being 10 times the horizontal; but the coral heads are exaggerated in horizontal scale in order to avoid giving a false impression of their shape. Here also, the time is that of low water of a low spring tide.

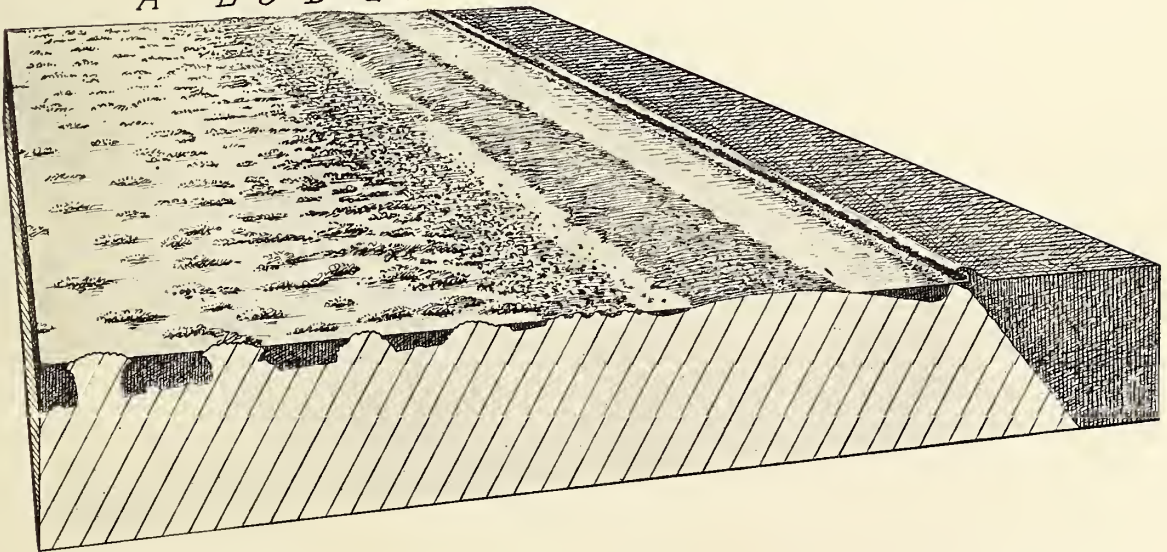


T.A.S. del.

FIG. 1.

- |                     |                 |
|---------------------|-----------------|
| A "ANCHORAGE" CORAL | E OUTER MOAT    |
| B BOULDER ZONE      | F OUTER RIDGE   |
| C INNER MOAT        | & BREAKERS      |
| D REEF CREST        | G PACIFIC OCEAN |

A B C D E F G



T.A.S. del.

FIG. 2.

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## DESCRIPTION OF PLATE XIX.

### FLORA OF LOW ISLES.

FIG. 1.—A typical growth of the flowering plant *Thalassia Hemprichii*, heavily colonized by the foraminiferan *Orbitolites complanata*.

FIG. 3.—The fleshy plant *Sesuvium Portulacastrum*, growing on the inner rampart.

FIGS. 2 and 4.—These figures illustrate the algal growth in the "trickle-zone" of the outer rampart, and also a certain degree of binding of the shingle by non-calcareous algae. Fig. 4 shows an almost pure growth of *Caulerpa racemosa*, fig. 2 a mossy algal turf chiefly composed of other forms.



*Photo S. M. Manton.*

FIG. 1.



*Photo G. Tandy.*

FIG. 2.



*Photo G. Tandy.*

FIG. 3.



*Photo G. Tandy.*

FIG. 4.

*Addard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE XX.

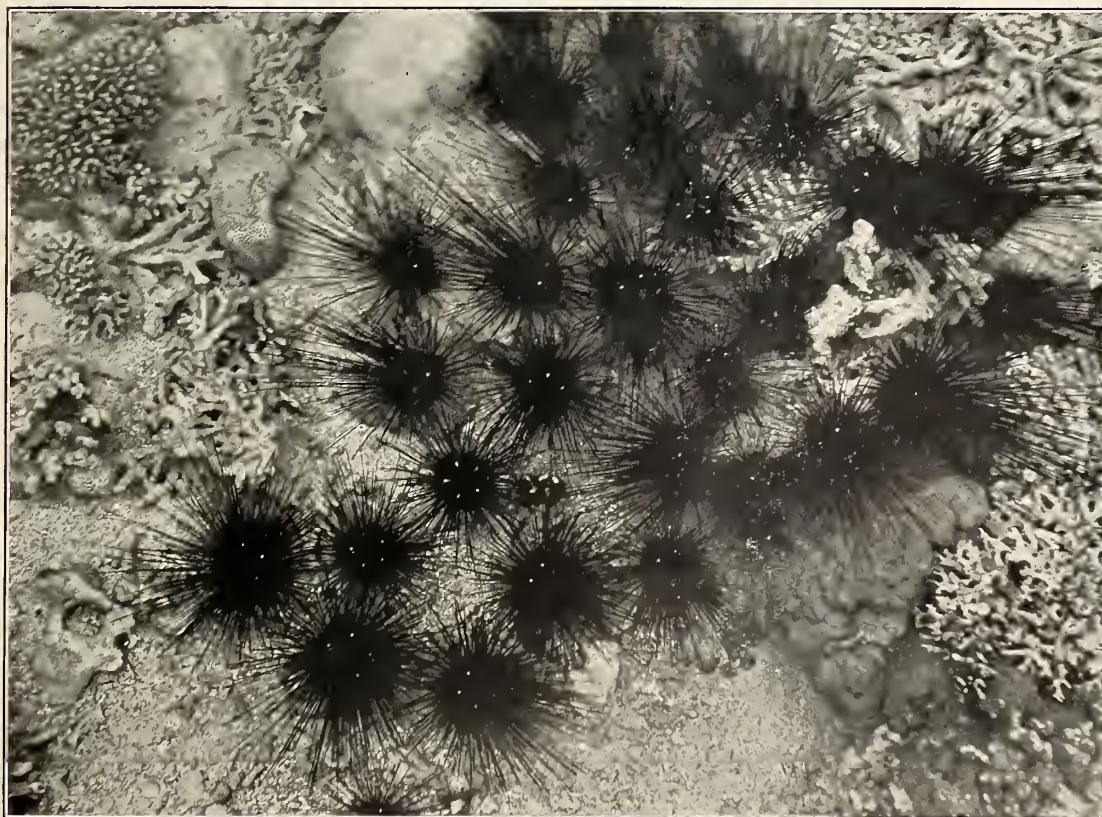
FAUNA OF LOW ISLES.

- FIG. 1.—The anemone *Actinodendron plumosum*. The body is buried in sand; the oral disc is produced into arms bearing branched tentacles. The animal was about 8 inches in diameter, and was coloured bright reddish brown.
- FIG. 2.—A colony of the urchin *Centrechinus (Diadema) setosus*, living in a moat. The individual urchins are about a foot across, and coloured deep purplish black. The pale spots visible on them in the photograph are in reality bright blue. The corals are massive *Porites*, *Pocillopora*, etc.



*Photo T. A. Stephenson.*

FIG. 1.



*Photo T. C. Roughley.*

FIG. 2.

*Adlard & Son, Ltd., Impr.*

## DESCRIPTION OF PLATE XXI.

### FAUNA AND FLORA OF LOW ISLES.

FIG. 1.—The convolvulus *Ipomaea Pes-caprae*, on the cay.

FIG. 2.—The chiton *Acanthozostera gemmata*, in the boulder tract. The length of the specimen was about 5 inches. The holes of boring organisms are also visible.

FIG. 3.—The baler *Melo diadema*, in the act of producing its egg-mass. The shell of this gastropod attains a length of 9 inches or more.

FIG. 4.—A colony of Zoanthids growing on a mangrove root, in the pond RP3. This species is common on the roots of *Rhizophora*. The polyps, which are half an inch or more in diameter, when in the condition here shown, are partly contracted because of the strong sunlight, although they are under water.



*Photo G. Tandy.*

FIG. 1.



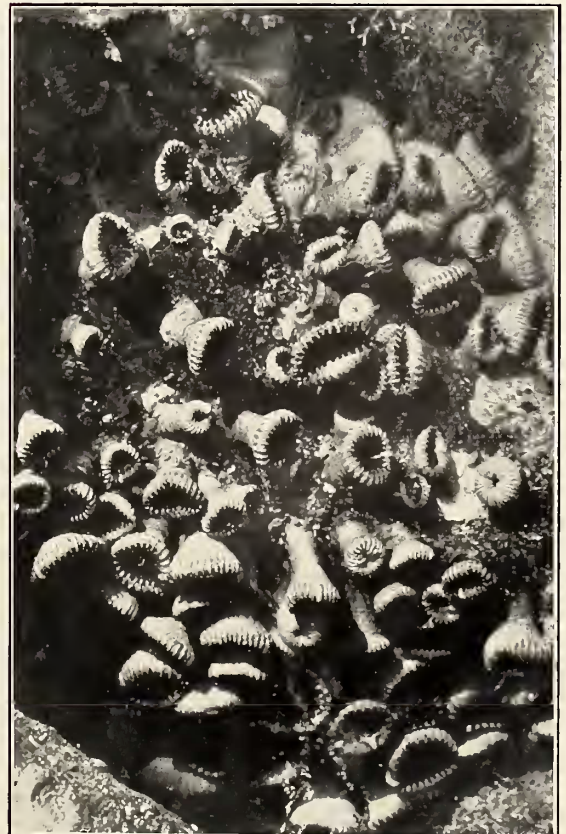
*Photo T. A. Stephenson.*

FIG. 2.



*Photo G. Tandy.*

FIG. 3.



*Photo T. A. Stephenson.*

FIG. 4. *Adlard & Son, Ltd., Impr.*



## DESCRIPTION OF PLATE XXII.

### THREE ISLES.

- FIG. 1.—The southern corner of the “high promenade” which lies to seaward of the dune and the mangrove swamp. The substratum in the foreground is “honeycomb-rock” overgrown by algae, etc.
- FIG. 2.—A closer view of the rocky promenade belonging to the Third Island, showing its pitted and eroded surface.
- FIG. 3.—A general view of the dune. The mainland can be seen in the distance (the two mountainous masses being the southern and northern parts of the Cape Bedford Peninsula), and the mangrove swamp would be to the right of the observer.



*Photo T. A. Stephenson.* FIG. 1.



*Photo T. A. Stephenson.* FIG. 2.



*Photo M. A. Spender.*

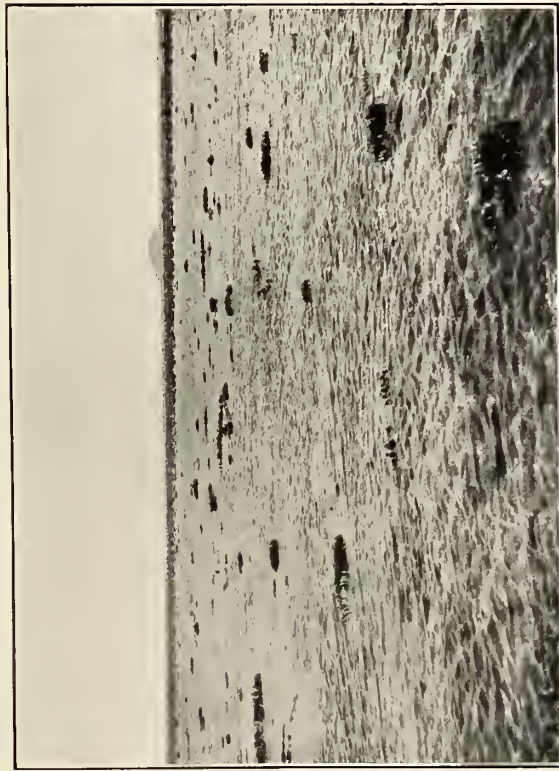
FIG. 3.

## DESCRIPTION OF PLATE XXVI.

### THREE ISLES, ARLINGTON REEF, LIZARD ISLAND AND YONGE REEF.

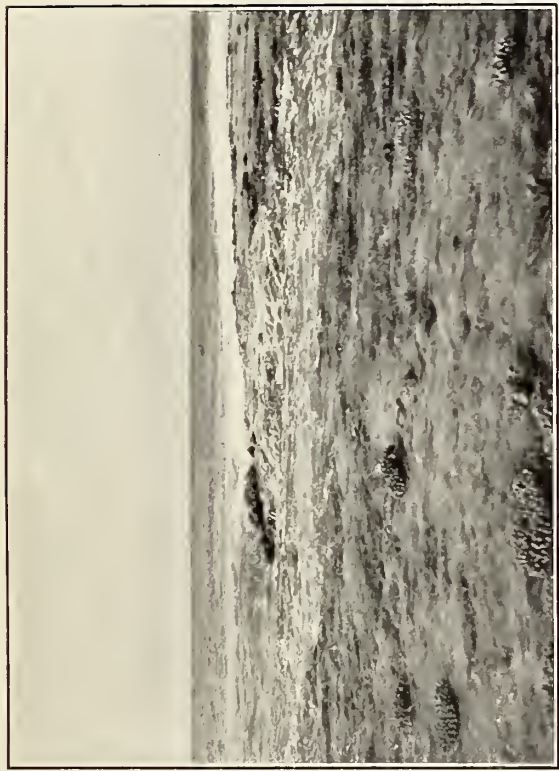
- FIG. 1.—Three Isles. A general view of the Third Island from its southern end. Three grades of vegetation are distinguishable (approximately). The low bushes in the foreground are mostly *Avicennia*; the darker ones of intermediate height on the left are other bushes (*Pemphis acidula*, *Osbornia octodonta*, or both); the tall trees are *Rhizophora*.
- FIG. 2.—Arlington Reef. A general view of the reef-flat. This photograph is included to illustrate the nature of the flat of a reef belonging to the Inner Series; it might equally well have been taken on Batt Reef.
- FIG. 3.—Lizard Island. View from the western slope of the mountain. Iguana Island is seen on the left, and between this and the foreground lies the western part of the shoal described on p. 87, with a number of reef-patches (clearly visible below the water as dark areas) on its surface.
- FIG. 4.—Yonge Reef. Madrepore field (see p. 84) at the southern end of the reef.

*Brit. Mus. (Nat. Hist.).*



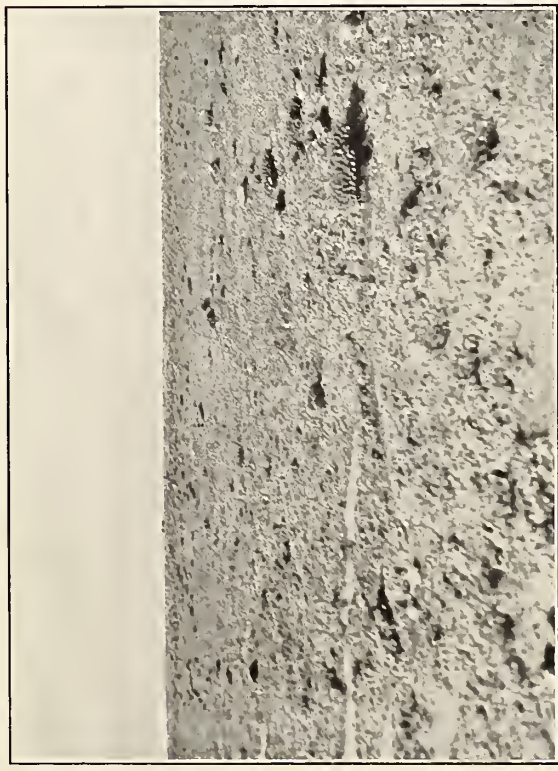
*Photo T. A. Stephenson.*

FIG. 1.



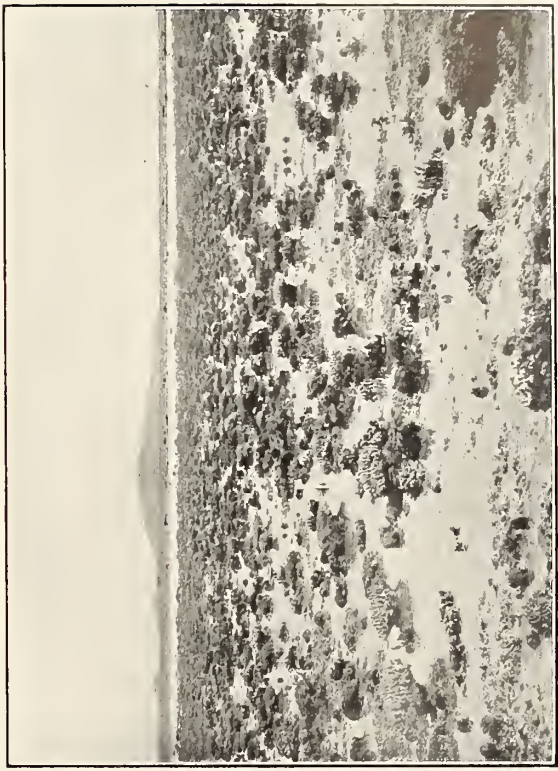
*Photo Anne Stephenson.*

FIG. 2.



*Photo Anne Stephenson.*

FIG. 3.



*Photo T. A. Stephenson.*

FIG. 4.

*Allard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE XXIV.

YONGE REEF.

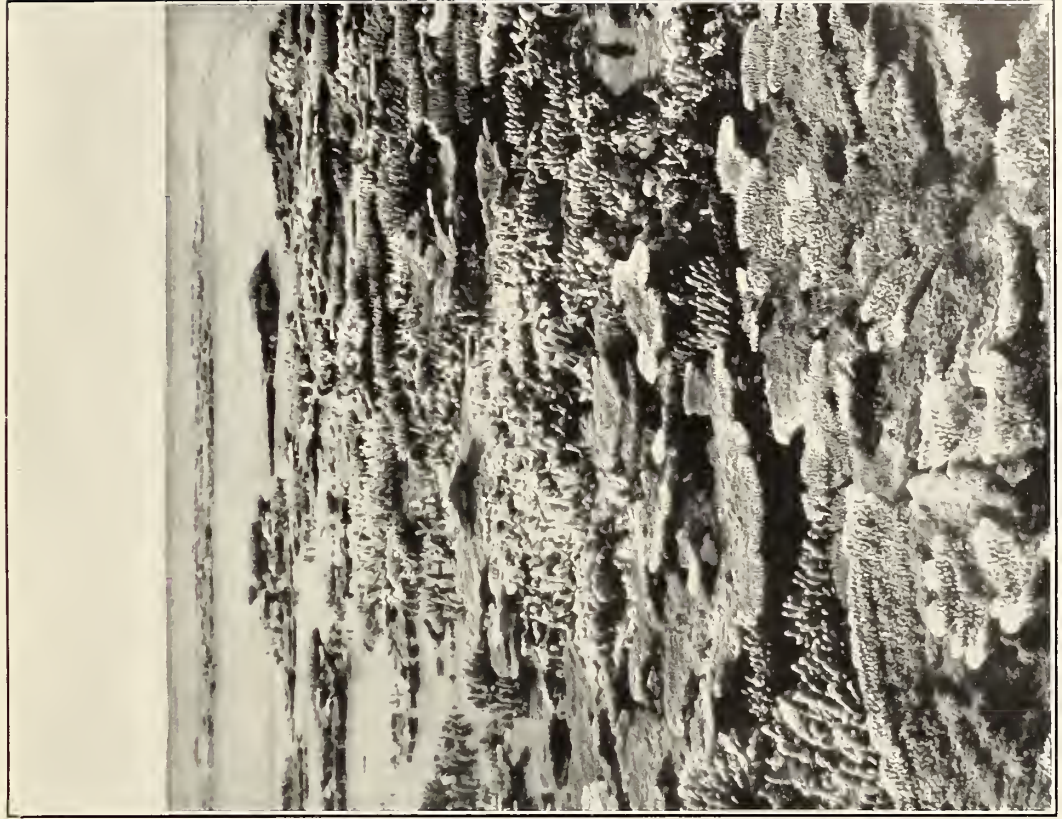
FIG. 1.—The anchorage coral zone. The observer is standing on the leeward side of the reef, looking towards the reef-crest.

FIG. 2.—Coral on one of the table-like "coral-heads" on the leeward side of the reef. The top of a second coral-head, like an island, is seen in the middle distance. Although this looks like a low reef, it is actually the top of a mass of coral with precipitous sides below the water. The channel between the foreground and the more distant coral-head was about three fathoms deep. The coral growth here is of about maximal density, and consists principally of species of *Acropora*, amongst which the bracket-like *A. hyacinthus* and the form with short thumb-like branches (*A. gemmifera*) are conspicuous.



*Photo S. M. Manton.*

FIG. 1.



*Photo T. A. Stephenson.*

FIG. 2.

*Adlard & Son, Ltd., Impr.*

## DESCRIPTION OF PLATE XXV.

### LIZARD ISLAND.

A sketch made from near the summit of the island, at a height of some 1100 ft. The foothills of Lizard Island form the foreground; the small islands are Newt and Iguana Islands; and between these and the foreground lies the system of reefs described on p. 87, and further illustrated in Text-fig. 6 and in Pl. XXVI, fig. 3. The three large distant reefs are Eagle Island, M reef, and L reef. In the background is the mainland, Capes Flattery and Bedford being visible. The position of Rocky Islets is indicated just below the horizon on the left.

GREAT BARRIER REEF EXPEDITION 1928-29.

*Brit. Mus. (Nat. Hist.).*

REPORTS, VOL. III, No. 2.

PLATE XXV.



*T. A. S. del.*

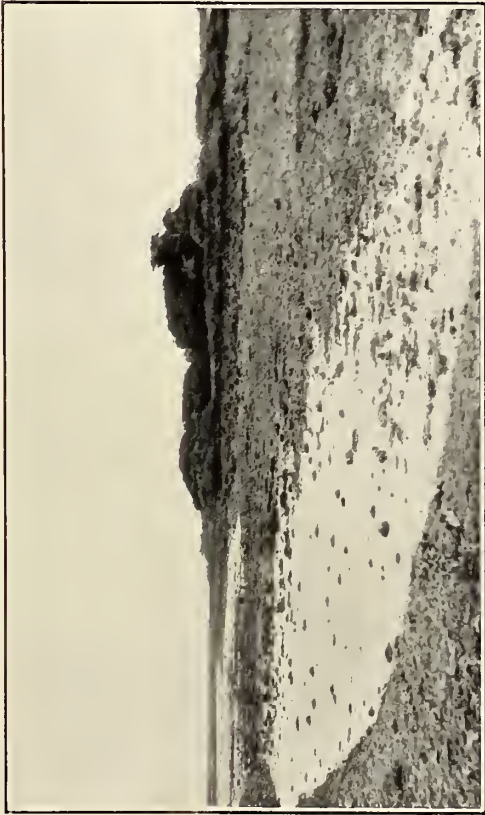
*Allard & Son, Ltd., Impr.*



## DESCRIPTION OF PLATE XXVI.

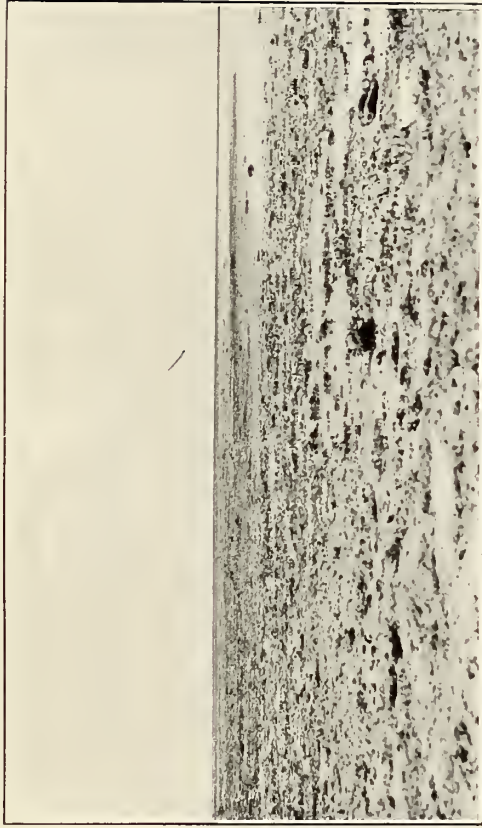
### THREE ISLES, ARLINGTON REEF, LIZARD ISLAND AND YONGE REEF.

- FIG. 1.—Three Isles. A general view of the Third Island from its southern end. Three grades of vegetation are distinguishable (approximately). The low bushes in the foreground are mostly *Avicennia*; the darker ones of intermediate height on the left are other bushes (*Pemphis acidula*, *Osbornia octodonta*, or both); the tall trees are *Rhizophora*.
- FIG. 2.—Arlington Reef. A general view of the reef-flat. This photograph is included to illustrate the nature of the flat of a reef belonging to the Inner Series; it might equally well have been taken on Batt Reef.
- FIG. 3.—Lizard Island. View from the western slope of the mountain. Iguana Island is seen on the left, and between this and the foreground lies the western part of the shoal described on p. 87, with a number of reef-patches (clearly visible below the water as dark areas) on its surface.
- FIG. 4.—Yonge Reef. Madrepore field (see p. 84) at the southern end of the reef.



*Photo M. A. Spender.*

FIG. 1.



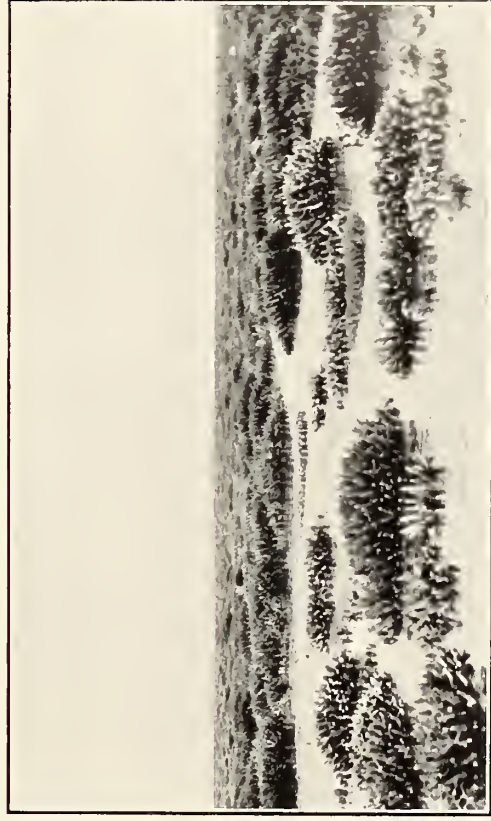
*Photo M. A. Spender.*

FIG. 2.



*Photo Anne Stephenson.*

FIG. 3.



*Photo M. A. Spender.*

FIG. 4.

*Allard & Son, Ltd., Impr.*

## DESCRIPTION OF PLATE XXIV.

### YONGE REEF.

- FIG. 1.—The anchorage coral zone. The observer is standing on the leeward side of the reef, looking towards the reef-crest.
- FIG. 2.—Coral on one of the table-like "coral-heads" on the leeward side of the reef. The top of a second coral-head, like an island, is seen in the middle distance. Although this looks like a low reef, it is actually the top of a mass of coral with precipitous sides below the water. The channel between the foreground and the more distant coral-head was about three fathoms deep. The coral growth here is of about maximal density, and consists principally of species of *Acropora*, amongst which the bracket-like *A. hyacinthus* and the form with short thumb-like branches (*A. gemmifera*) are conspicuous.

IR3 P10 IM3 THE LONG TONGUE IM2 GREEN ANT ISLAND IM4 IM4B IM4A IM5



OUTER RAMPART SESUVIUM  
TRICKLE ZONE HONEYCOMB ROCK

M7 (POOL)

INNER RAMPART

NEW SHINGLE-WAVE  
PHOTOGRAPHS BY R.A.A.F.